Release from sheep-grazing appears to put some heart back into upland vegetation: a comparison of nutritional properties of plant species in long-term grazing experiments

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Removal of sheep grazing and impacts on plant nutritional value

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Abstract

(Re)-wilding is a popularised means for enhancing the conservation value of marginal land. In the British uplands, it will involve a reduction, or complete removal, of livestock grazing (sheep), based on the belief that grazing has reduced plant species diversity, the 'Wet Desert' hypothesis. The hope is that if livestock is removed, diversity will recover. If true, we hypothesise that the species extirpated/reduced by grazing and then recovering on its removal would more nutritious compared to those that persisted. We test this hypothesis at Moor House National Nature Reserve (North-Pennines), where seven sets of paired plots were established between 1953 and 1967 to compare ungrazed/sheep-grazed vegetation. Within these plot-pairs, we compared leaf properties of seven focal species that occurred only, or were present in much greater abundance, in the absence of grazing to those of ten common species that were common in both grazed and ungrazed vegetation. Each sample was analysed for macro-nutrients, micro-nutrients, digestibility, palatability and decomposability. We ranked the species with respect to twenty-two variables based on effect size derived from Generalised Linear Modelling (GLM) and compared species using a Principal Components Analysis. We also assessed changes in abundance of the focal species through time using GLMs. Our results support the 'Wet Desert' hypothesis, i.e. that long-term sheep grazing has selectively removed/reduced species like our focal ones and on recovery they were more nutritious (macro-nutrients, some micro-nutrients) palatable, digestible and decomposable than common species. Measured changes in abundance of the focal species suggest that their recovery will take 10-20 years in blanket bog and 60 years in high-altitude grasslands. Collectively, these results suggest that sheep grazing has brought about biotic homogenization, and its removal in (re)wilding schemes will reverse this process eventually! The 'white woolly maggots' have eaten at least part of the heart out of the Highlands/uplands, and it will take some time for recovery.

Introduction

Rewilding or wilding are terms that describe a range of management approaches, ranging from the introduction of wide-ranging large animals, especially top carnivores (Soulé & Noss, 1998), through to the abandonment of land, and a reduction in stock-grazing pressure (Merckx & Pereira, 2015; Corlett, 2016). The effects of stock grazing pressure were first identified in the United Kingdom by Frank Fraser Darling, who coined the term "wet desert" to describe the species-poor vegetation of the Scottish Highlands, which he ascribed to a high, long-term, sheep-grazing pressure (Darling, 1955; Stewart, 2010; Crumley, 2000). Monbiot (2013) continues this debate, arguing that the British uplands are species-poor wastelands, "sheep-wrecked", because of the high sheep-grazing pressure. In this situation, sheep are often referred to as "white woolly maggots" or "hoofed locusts" that "have eaten the heart out of the Highlands/uplands" (Toogood 1995; Monbiot, 2013; Baroness Young of Old Scone, pers. comm.).

If it is true that high sheep grazing has reduced species diversity, this can be translated into two hypotheses. First, that the historic high grazing pressure has removed certain species selectively (biotic trait homogenization, Smart *et al*., 2005, 2006), and second that removal of that grazing pressure will allow those species to return. If this were to be the case, we would predict that:

(1) Species that have survived grazing will tend to have similar traits with respect to nutritional value, digestibility and palatability,

(2) The species extirpated or reduced by grazing will have greater nutritional value, be more digestible and palatable and because of the higher nutritional status, they will decompose much faster.

We can test these hypotheses by comparing the response of vegetation where sheep grazing can be compared with comparable ungrazed areas, usually within fenced exclosures. A good example of a series of such exclosure studies are those set up on the Moor House NNR in the North of England between 1953 and 1967 (Marrs *et al*., 1986; Milligan *et al*., 2016). These experimental plots are distributed across the reserve; each compares sheep-grazed and ungrazed comparator plots, thus allowing an assessment of the effects of grazing removal on a range of plant community types encompassing a large proportion of British upland plant communities (Rodwell, 1991, 1992; Averis *et al*., 2004). The plant communities included vegetation dominated by dwarf-shrubs, grasses and sedges, growing on soils ranging from deep blanket peat through to brown-earth soils, and subject to very different, and indeed changing, sheep grazing pressures, which were related to forage quality (Eddy *et al.*, 1968; Rawes & Welch, 1969). These vegetation types, in common with elsewhere in upland Britain, are described as degraded by sheep overgrazing (Darling, 1955; McGovern *et al.*, 2011).

A first assessment (Marrs *et al*., 2018) of both soils and the quality of the total herbage (macro-nutrients and digestibility) in eight of these experiments showed almost no difference in macro-nutrient concentrations or digestibility. The only significant result was for one of the digestibility measures (acid detergent fibre concentration, ADF), which was lower where sheep were removed, indicating the vegetation had become more digestible (Marrs *et al*., 2018). However, although there were few differences at the vegetation scale (total herbage), it was obvious that some species had either colonised or increased markedly in abundance within the ungrazed plots compared to those sheep-grazed (Milligan *et al*., 2016). Where sheep continued to graze, there was a reduction in species diversity and in the abundance of vascular plants, grasses, lichens, liverworts and mosses; but an increase in herbs, sedges and shrubs. Removal of sheep grazing reduced the abundance of grasses and liverworts compared to their grazed counterparts but herbs, mosses, sedges and shrubs all increased (Milligan *et al*., 2016). The species that have increased after grazing removal are presumably those that have been reduced or extirpated by sheep grazing, and have recovered as a result of the zero sheep grazing pressure

Here, we capitalise on these long-term experiments by comparing the traits of seven species (here termed focal species), which have either colonised the ungrazed plots since grazing ceased, or have become much more abundant than under grazed conditions, with ten common species that occur widely in both grazed and ungrazed plots. For each species, we measured the concentrations of macro-nutrients, micro-nutrients, dry matter, fibre, lignin, protein and surrogate measures of metabolizable energy, digestibility (Si) and decomposability (C: N ratio). If our two hypotheses were correct, we would expect the seven focal species to be more nutritious, palatable, digestible and be capable of decomposition faster than the common species that have survived sheep-grazing. At the same time, we quantified the time taken for focal species to become abundant after grazing stopped.

Methods

This study used seven sheep-exclosure experiments located across the major moorland vegetation types found across Moor House National Nature Reserve in the northern Pennines of England (Fig. S1). These experiments were set up between 1953 and 1967 and designed to assess the impact of stopping sheep grazing (ungrazed exclosure) relative to free-range, sheep grazing. The vegetation types covered were representative of many upland ecosystems found in much of upland Britain with six NVC plant community types included (Table S1). These communities cover ca. 80% of this reserve where they are grazed at a range of sheep densities (Table S1).

It is important, however, to realize that whilst long-term effects of sheep grazing *versus* no grazing are visible at these sites, the background grazing pressure has not been static. The reserve is a Common under English law, which means that designated farm-holdings from outside the moorland have the "right" to graze their sheep on the land. In the late 1960s, detailed studies by Rawes and Welch (1969) estimated 15,400 sheep on the reserve in the summer months; assuming a grazing area of 3,500 ha, this averages 4.4 sheep ha^{-1} across all vegetation types. In 1972, after the formalization of grazing-rights for Moor House under the Commons Registration Act (1965), grazing density reduced >50% to 7000 sheep or 2 sheep ha^{-1}. In the early 2000s, buy-out of some of the common rights-of-grazing led to further reductions in sheep numbers to ca. 3500 sheep or one sheep ha^{-1} (Milligan *et al*., 2016, 2018). The conservation objective for these reductions was the hope that it would lead to an improved vegetation quality. Rawes and Welch (1969) also showed that sheep grazing pressure in the plant communities available to the sheep was not random, with 11.6-23.2% greater densities on the most-grazed grassland communities compared to the least-grazed Blanket bogs (Table S1). Changing pollutant loads (SO_2 and NO_x) have also varied during this time and may also have affected species responses (Monteith *et al*. 2016; Rose *et al*., 2016). Hence, our experiments reflect an assessment of the effects of no sheep grazing relative to a dynamic "business-as-usual" grazed scenario where the grazing pressure has reduced (Milligan *et al*., 2016, 2018).

Vegetation sampling

At the end of July 2016, the seven experiments were visited, and individual species sampled in two groups based on visual inspection of the plots. Group 1 denoted here, as common species were present in reasonable abundance in both grazed and ungrazed plots. Some species (Group 1a) were found in only one experiment and comprised: *Carex bigelowii*, *Nardus stricta*, and *Vaccinium myrtillus. Juncus squarrosus* was also sampled in the ungrazed plot on one experiment. Others (Group 1b) were present in both grazed and ungrazed plots in more than one experiment, and comprised *Calluna vulgaris*, *Avenella flexuosa*, *Empetrum nigrum, Eriophorum vaginatum* and *Galium saxatile* (Plant nomenclature follows Stace, 2019).

Group 2 denoted here as focal species, were either present or abundant in the ungrazed plot of one experiment but were absent from, or present in very low abundance in, the grazed plots. This group comprised *Dryopteris dilatata,* which was present at low densities, and six species that were present in abundance (*Chamaenerion angustifolium*, *Geum rivale*, *Narthecium ossifragum*, *Potentilla erecta*, *Rumex acetosa* and *Rubus chamaemorus*) in at least one ungrazed plot.

For all species, three patches were selected randomly and plant parts harvested; shrubs = new annual shoots, graminoids = green leaves, dicotyledons = new shoots, fern = whole frond. In the laboratory, the samples were oven-dried at 80^{o}C for 48h and milled to pass a 1mm mesh.

Chemical analyses

Total N and C determinations were made using a Thermo Scientific Flash 2000 Organic Elemental Analyser. For P and cations (K, Na, Ca and Mg), plant samples were analysed using the dry-ashing method (Allen, 1989). P was analysed by colorimetry (P) using a Seal Analytical AA3 HR AutoAnalyser and cations by absorption (Ca and Mg) and emission spectrophotometry (K and Na) on a Thermo Electron Corporation Solaar S4 AAS. The C:N ratio was used as a surrogate measure for decomposability.

Micro-nutrients

Micro-nutrient element concentrations (Cl, Co, Cr, Cu, Fe, Mn, Mo, Ni, S, Si, Zn) were determined on the plant samples after using an Energy Dispersive X-ray Fluorescence Analyser (ED-XRF). Dried samples were pressed (1.5 t) in 20 mm pots, and measured under a He atmosphere using a Spectro XEPOS 3 ED-XRF that emits a combined binary Pd and Co excitation radiation and uses a high resolution, low spectral interference silicon drift detector. The XRF analyser undergoes a daily standardization procedure, with accuracy verified using 18 certified reference materials (Boyle *et al*. 2015). Si concentration was used as a surrogate measure of palatability (Massey *et al*., 2009; Moise *et al*., 2019).

Digestibility

All samples were lightly hand pressed (Korsman *et al*., 2001), and Near Infrared Reflectance (NIR) spectra measured by diffuse reflectance using an integrating sphere on a Bruker MPA Fourier-Transform NIR spectrometer based on combining 64 scans collected at 8 cm-1 intervals across the range 3595–12,500 cm^{-1}. The NIR spectra were analysed using OPUS spectroscopy software (v. 6.5, Bruker, 2018) and the individual nutritional components (Dry Matter, ADF, NDF, DOMD (Digestible Organic Matter in Dry Matter a surrogate measure for Metabolizable Energy) quantified using ready-to-use INGOT® calibration applications for forages from Aunir (AB Agri., Towcester, Northamptonshire, UK). Crude protein was calculated as x6.25 the N concentration (Van Soest, 1994)

Statistical analysis

All statistical analyses were performed in the R statistical environment (R Core Team, 2017); the 'vegan' package was used for the multivariate analyses (Oksanen *et al*., 2019).

Initially, the common species were tested for differences in leaf properties between grazed and ungrazed plots. Where a common species was collected at only one site (Group 1a), differences in leaf properties between samples collected in the grazed and ungrazed plots were tested using a t-test ('t.test' function). Where a common species was collected at more than one site (Group 1b), differences in leaf properties were tested using analysis of variance ('aov' function) using sites and grazing treatment as factors. Of the 168 grazed *versus* ungrazed contrasts (both t-tests and aov) only three produced a significant difference between grazed ad ungrazed treatments ($P<0.01$), with *A. flexuosa* having greater concentrations of Ca, Fe and Mn in grazed plots compared to ungrazed ones (Table S2). Accordingly, *A. flexuosa*, was treated as two species (*A. flexuosa*-G and *A. flexuosa*-U) for the analyses for these three elements and the multivariate analysis. Otherwise, as there were no other significant differences between grazed/ungrazed plots, all data for common species were pooled in all other analyses.

Generalized linear models (GLM) were used to investigate the relative differences in leaf nutritional properties between species. The GLMs were, therefore run with species as a fixed factor and as the variables were all continuous ones, a Gaussian error structure was used with transformed data (elements = $\log_e(x)$ and percentages (digestibility variables =asin(sqrt(x/100)). For five variables where a high value represented low nutritional quality (C, ADF, NDF, Si concentrations and C:N ratio), the model intercepts were set to the species with the largest mean value. All other species were then ranked in graphs by effect size (estimate) away from this intercept (an example of this analysis is presented in Fig. 1a for ADF). For all other variables, a similar approach was used except the intercepts were set at the species with the lowest mean value, i.e. the species with the least nutritional value (an example of this analysis is presented in Fig. 1b for Mg concentration). The approach allowed the spectrum of response to be ranked in terms of nutritive value from the worst to the best species. Assuming the hypothesis is accepted, i.e. that the focal species were more nutritious/digestible/palatable/ decomposable than the common species then the focal species should be ranked 1-7 out of the 17 species assessed (18 when Df-G and Df-U were separated) and be plotted at the positive end of the graph. The graphs for all variables are presented as Supplementary Fig. S2 and all statistical outputs are presented in Supplementary Tables S3-S6. For brevity, the discussion centres around a summary table of ranks, derived from these individual analyses for each focal species, assessed against their respective intercept.

In addition, the difference between the focal and common species groups were also analyzed for each variable using GLM using the same analytical methodology except that species group was the fixed factor (i.e. common *versus* focal). These statistical outputs are presented in Supplementary Table S7.

In addition, in order to summarize all the measured variables in one analysis, the combined dataset (macro-, micro-nutrients, digestibility, palatability and decomposability) were analysed together using principal components analysis (PCA), an unconstrained ordination technique using the 'rda function after standardization (mean=0, s^2=1) using the 'decostand' function. The relative positions for each species on the biplots were visualized using standard-deviational ellipses with 95% confidence intervals, fitted using the 'ordiellipse' function.

For the temporal assessment, the abundance values for the focal species were abstracted from the Moor House Grassland Monitoring Database for each experiment. These data were collected using pin quadrats within random quadrats (Marrs *et al*., 1986). The species abundance in each grazed and ungrazed plot were summed at quadrat level for each year and modelled against time. GLM modelling was described as above but as the data were counts a Poisson error structure with a log-link function was used (Crawley, 2013). The statistical outputs are presented in Supplementary Table S8.

Results

Comparison of the nutrition of focal and common species

Macro- and micro-nutrients

All of the focal species were ranked in the top 7 (out of 17) in terms of nutritional quality for at least two macro-nutrients, and all had greater (lower for C) concentrations than the intercept species (Fig. S2, Table S.3,). *R. chamaemorus* and *N. ossifragum* had the least with only two elements in the top seven, Ca and Mg for the former and N and Na for the latter. *D. dilatata*, *P. erecta* and *R. acetosa* had six and *C. angustifolium* had all seven in the top ranks (Table 1). Importantly, each species had a different combination of elements that were greater in the top ranks (Table 1). The focal species group had significantly greater concentrations than the common species group for all macro-nutrients elements except C, which was significantly lower (Table 1).

Compared to macro-nutrients the pattern for the micro-nutrients was less clear with some species for some elements showing no significant difference from the intercept species (Table 1, Fig. S2, Table S4). *D. dilatata* was in the top seven out of eight elements (Cl, S, Mn, Fe, Cu, Zn and Ni), *R. acetosa* for six elements (Cl, S, Fe, Mn, Fe, Cu, and Ni), *C. angustifolium* and *N. ossifragum* for five each (Ca = Cl, S, Mn, Cu, and Zn; No = Cl, S, Mn, Cr, and Mb), *R. chamaemorus* for three (Cl, S and

Mn) and *G. rivale* was rankled in the top seven only for Cl. Note that *N. ossifragum* was the only focal species ranked in the top seven for Mb. *P. erecta* was not in the top seven for any element, the highest rank achieved was eighth for Mn and Zn. The focal species group had significantly greater concentrations (P<0.10) than the common species for Cl, S, Mn and Zn, and lower concentrations of Fe, Cu, Ni, and Mb, with only Mb being significant (P<0.001, Table 1).

Digestibility

Here, there are two things to consider, (1) the fibre concentrations (ADF, NDF), and (2) the quality of the plant material, assessed through DOMD (a surrogate energy measure) and protein concentration.

For fibre, five species (*C. angustifolium*, *G. rivale*, *N. ossifragum*, *P. erecta*, R. acetosa (ADF only) and *R. chamaemorus*) were ranked in the top seven, i.e. they had lowest concentrations of ADF, NDF or both (Table1, Fig. S2, Table S5), indicating that they are more digestible than the common species. All were significantly less than the intercept species (P<0.001). *D. dilatata* was ranked twelfth and eighth for ADF and NDF respectively and *R. acetosa* was ranked fifteenth for ADF.

In terms of energy and protein concentrations all focal species had significantly larger DOMD and protein values than the intercept species (P<0.001). Five of the seven focal species were in the top seven for DOMD (*C. angustifolium*, *G. rivale*, *N. ossifragum*, *P. erecta*, *R. chamaemorus*) and protein (*C. angustifolium, D. dilatata*, *G. rivale*, *N. ossifragum*, *R. acetosa and R. chamaemorus*) indicating either higher energy and protein values (or both) than the common species (Table1, Fig. S2, Table S5).

The focal species group had significantly lower concentrations of ADF and NDF and greater concentrations of DOMD and protein than the common species (Table 1).

Decomposability and Palatability

All focal species were significantly different from the intercept (P<0.001) for both Si concentration (P<0.001) and C:N ratio (P<0.001) (Table 1, Fig. S6, Fig. 2). For palatability (Si concentration), five of the seven focal species (*C. angustifolium*, *D. dilatata, G. rivale*, *N. ossifragum* and *R. acetosa*) were ranked in the top seven, and for decomposability (C:N ratio), but six (*C. angustifolium*, *D. dilatata, G. rivale*, *N. ossifragum, P. erecta* and *R. acetosa*) were ranked in the top seven (Table 1). The focal species group had significantly lower Si concentrations and C:N ratios than the common species indicating greater palatability and decomposability (Table 1).

Multivariate analysis

The PCA produced eigenvalues of 7.477 and 3.174 for the first two axes explaining 51% of the total variation in the dataset. The biplots show a clear gradient along the first axis from low-quality vegetation (C, C:N, ADF and NDF) at the negative end through to more nutrient- and energy-rich vegetation at the positive end (Fig. 2a). On the second axis, the gradient runs from high fibre (NDF), Si and micro-nutrients (Cu, Mb, Mn, Ni, and S) at the positive end through to high protein and Ca and Mg at the negative end (Fig. 2a).

The species distribution reflects this with most of the common species being mainly located either at the negative end of axis 1 or in the upper right quadrant; the exception being *G. saxatile* which straddles the positive end of axis 1 (Fig. 2b). The focal species are all located in the lower right quadrant, indicating correlations with high energy, protein, N, P, Ca, Mg, Na, K and micro-nutrients (Fig. 2b).

Species change through time

Two focal species showed no significant change through time. *D. dilatata* was patchily-distributed and was below the detection limits of the sampling methodology and *C. angustifolium* showed an increase in abundance after 60 years in the enclosed plot but no significant temporal relationship. Of the remaining five focal species, only *N. ossifragum* showed a slight increase in the sheep grazed plots, no relationship could be fitted for the other four species when sheep grazed (Fig. 3). The responses of the three species found predominantly in grasslands (*G. rivale*, *P. erecta* and *R. acetosa*) were relatively small when grazing was removed, with increases being detectable after 60 years (Fig. 5). The two species found in predominantly *Calluna-Eriophorum*-dominated vegetation (*N. ossifragum* and *R. chamaemorus*) showed greater and faster increases after sheep grazing was removed, i.e. over a ten to twenty-year period (Fig. 3).

Discussion

This study confirms observations and predictions made over the last century about the impact of extensive sheep grazing in upland Britain and supports our two hypotheses. This has been achieved through a combination of comparisons of nutritional status of a range of plant species within long-term experiments on the effects of sheep removal compared to the business-as-usual grazing pressure and monitoring species recovery. Analysis of the nutritional properties, ranked species on twenty-two variables, covering macro- and micro-nutrient concentrations and measures of digestibility, palatability and decomposability was done by a simple ranking procedure based on the effect sized derived from a GLM model and multivariate analysis. These analyses collectively showed that sheep grazing has selectively removed or reduced species like our focal ones, and the common

species that persist have similar plant traits in terms of nutrient composition, palatability and digestibility. Moreover, the higher C:N ratio of the common species suggests that they will decompose more slowly and act as a negative feedback on primary production. Second, when sheep grazing was removed, the focal species, i.e. those that either colonized or increased markedly in the exclosures, were more nutritious in terms of at least some macro-nutrients, digestibility and palatability; a few also had greater concentrations of some micro-nutrients. Moreover, their lower C:N ratio suggests that where present they would decompose faster and produce a positive feedback on production. These local increases in abundance could contribute to reversing biotic/trait homogenization (Smart *et al*., 2005, 2006). The larger Ca and/or Mg concentrations in six of the seven focal species, and their improved digestibility, relative to the common ones is consistent with Mladkova *et al*. (2018), who suggested that high values of these elements increases digestibility. This is partly associated with evolutionary development and the differential concentrations of these elements in cell walls (White *et al.,* 2018). High concentrations of Ca and Mg have also been used as indices of litter decomposition rate (Cornelissen & Thompson, 1997).

Taken together, the results support Frank Fraser Darling's (1955) "wet desert" hypothesis and Monbiot's (2013) view of upland degradation, in that nutritious plants are selectively removed/reduced by sheep. It also suggests that relaxation of the grazing pressure will allow species that have extirpated or reduced to recover, but if the rates from these experiments at Moor House are typical then this will take some time; 20-40 years on blanket bog and 60 years for high-altitude grasslands. It should also be noted that increasing *N. ossifragum* may prove problematic if there were any stock grazing around as it is highly poisonous (Angell & Ross, 2011) as a result of a toxic component identified as 3-methoxy-2(5H)-furanone (Langseth *et al*., 1999). The faster recovery of blanket bog species might be because the stock grazing pressure on this vegetation type is lower than grasslands (Table S1, Rawes & Welch, 1969). Hence, the degradation of vegetation in terms of species loss might be slower, it might not reach as low a base, and hence recovery is faster; this hypothesis remains to be tested. At least some of the heart has been eaten out of the Highlands/uplands, and it will take some time to replace it.

Limitations on the use of exclosures

There are several drawbacks to the approach of merely comparing the change in vegetation in sheep-free exclosures versus the business-as-usual sheep grazing pressure. First, the use of exclosures means that the sheep grazing pressure is set at zero and hence no information can be derived on impacts of very low grazing pressures that might be associated with (re)wilding schemes. Second, we know that the business-as-usual stock grazing pressure has been reduced at the

landscape scale during the experimental period, and possibly from a higher historic base in the 19th century (Darling, 1955). Historic changes in sheep numbers in the north Pennines show opposing trends. For example, at the nearby Shap estate, sheep numbers reduced from ca. 23,000 to 5,600 in the 1940s, but at lower altitudes in Lunedale, there was a steady increase in sheep numbers from 5,000 to 12,700 between 1900 and 1960 (Ball *et al*., 1982). These reductions will almost certainly have intensified differences in grazing pressures between the different vegetation types brought about by sheep selection (Table S1), for example by maintaining a high pressure on the more-productive grasslands but reducing it on the least-productive blanket bogs (Eddy *et al*. 1968; Rawes & Welch, 1969). Third, it is likely that although there is no stock grazing within the exclosure it is possible that compensatory grazing by small mammals or insects may impact on species change trajectories and nutrient turnover (Chen *et al.,* 2019; Linabury *et al*., 2019; Poe *et al*., 2019). There are few, if any, mega-herbivores such as deer in the Moor House grazing unit at present. Fourth, the exclosures used here are of relatively small-scale (<1200 m^2) in comparison to the potential scale of the area available on this grazing unit, ca. 3,500 ha. Lastly, the focal species were to some extent self-selecting in that they were the most obvious ones showing an increase in the exclosures in 2015. We accept that this is a very small selection of species that could have been chosen. Hence, here, we acknowledge that our results are indicative of potential changes associated with sheep removal and only provide a first approximation of likely impacts and timescales. Further, more detailed work is needed on these processes, both at Moor House, and elsewhere.

Implications of these results

These results have important implications in terms of ecological theory and conservation management practice.

From a theoretical perspective, the focal species have larger quantities of at least some nutrients in their tissues. There were no significant differences in soil chemical properties between any of the grazed and exclosure plots when sampled in 2015 (Marrs *et al*., 2018). As a consequence, the focal species must either be able to extract nutrients in a more efficient way than the common species from the same soil resource and/or they invest resources into more palatable\digestible tissues making them more susceptible to grazing. That species have differing elemental compositions is well known (Lambers & Poorter, 1992; Thompson *et al*., 1997), and reflects evolutionary status, and differences in root characteristics, relative growth rates, root:shoot ratios, rhizosphere interactions, improved mycorrhizal associations, absorption processes, foraging behaviour or differential resource allocation within the shoots (Chapin, 1980; Hutchings & de Kroon, 1994; Thompson *et al*., 1997). It remains unclear whether internal plant physiological functions, mycorrhizal or rhizosphere interactions brought about these increased elemental concentrations. The relative relationship

between fungal and bacterial communities at the micro-level may also be affected by the colonization by these focal plant species; low fertility soils tend to be fungal-dominated, higher fertility soils bacterial-dominated (Smith *et al*., 2003; de Vries *et al*., 2012). Reductions in airfall acid deposition in these upland communities (Rose *et al*., 2016) may also have affected the species responses. Further studies are needed to elucidate the exact mechanisms involved.

From a conservation management perspective, the removal of grazing livestock in (re)wilding schemes should eventually increase plant species diversity, but it may as seen here take a considerable time. There are at least two potential constraints. The first is one of seed limitation. We have very little information on the potential for species dispersal into these large areas, or on the existing seedbanks, which may or may not contain a legacy of potential colonists. If management wishes to accelerate the colonization of new species, then it may be necessary to add seed (Miles, 1974; Hester *et al*., 1991 Mitchell *et al*., 2008). The second constraint is the lack of "safe-sites" (Harper, 1977); bare gaps necessary for the seed to germinate and establish. The herbage mass in these experiments range form 850-2,900 g m^{-2} (Marrs *et al*., 2018), and almost certainly this vegetation will prevent seeds getting into the soil pool (Ghorbani *et al*., 2006) and subsequently germinating (Miles 1974; Lowday & Marrs, 1992). A range of approaches could be used to create these gaps by disturbing the extant vegetation including the use of herbicides, fire or physical damage by cutting, rotavating or screefing (Miles, 1974; Humphrey & Coombs, 1997; Milligan *et al*., 2004; Lee *et al*., 2013).

Experimental research to develop integrated approaches combining disturbance with seed addition will be needed if the intended objective is to accelerate (re)wilding as part of a conservation management strategy.

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Conflicts of Interest

RHM is the President of the Heather Trust - a Scottish charity aimed at reconciliation in upland management. This is a non-executive appointment with no decision-making powers. He also sits on Natural England's Upland Management Group and the Game & Wildlife Trusts Uplands Science Advisory Committee. All roles are unpaid

References

Allen, S.E., ed. (1989). *Chemical Analysis of Ecological Materials, 2nd edn*. Blackwells, Oxford, UK.

Angell, J., Ross, T. (2011). Suspected bog asphodel (*Narthecium ossifragum*) toxicity in cattle in North Wales, *Veterinary Record*, **169**, 101b. doi: 10.1136/vr.d3879.

Averis, A.B., Averis, A.M., Birks, H.J.B., Horsfield, D., Thompson, D.B.A., Yeo, M. (2004). *An Illustrated Guide to British Upland Vegetation*. Joint Nature Conservation Committee, Peterborough, UK.

Ball. D.F., Dale, J., Sheail, J., Heal, O.W. (1982). *Vegetation change in upland Britain*. Institute of Terrestrial Ecology, Bangor, UK.

Boyle, J., Chiverrell, R., Schillereff, D. (2015). Approaches to water content correction and calibration for µXRF core scanning: comparing x-ray scattering with simple regression of elemental concentrations, in *Micro-XRF studies of sediment cores: A non-destructive tool for the environmental sciences. Developments in Paleoenvironmental Research* (Eds Rothwell, G. and Croudace, I.). pp. 373-390. Springer, Dordrecht.

Bruker (2018). Opus Spectrocsopy Software v.6.5. Bruker, Coventry, UK. https://www.bruker.com/products/infrared-near-infrared-and-raman-spectroscopy/opus-spectroscopy-software.html. [Accessed 1/4/2019].

Chapin, F.S. (1980). The mineral nutrition of wild plants. *Annual Review of Ecology & Systematics*, **11**, 233-260. DOI: 10.1146/annurev.es.11.110180.001313.

Chen, Q., Howison, R.A., Bakke,r J.P., Alberti, J., Kuijper, D.P.J., Olff, H., Smit, C. 2019. Small herbivores slow down species loss up to 22 years but only at early successional stage. *Journal of Ecology*, https://doi.org/10.1111/1365-2745.13236.

Corlett, R.T. (2016). Restoration, reintroduction, and rewilding in a changing world. *Trends in Ecology & Evolution,* **31**, 453-462. DOI: 10.1016/j.tree.2016.02.017.

Cornelissen, J.H.C., Thompson, K. (1997). Functional leaf attributes predict litter decomposition rate in herbaceous plants. *New Phytologist*, **135**, 109-114. DOI: 10.1046/j.1469-8137.1997.00628.x.

Crawley, M.J. (2013). *The R Book, 2nd edn.* John Wiley and Sons, Chichester.

Crumley, J. (2000). *A High and Lonely Place: Sanctuary and Plight of the Cairngorms*. Whittles Publishing, Dunbeath, Caithness, Scotland.

Darling, F.F. (1955). *West Highland Survey: an essay in human ecology*. OUP, London, UK.

de Vries, F.T., Bloem, J., Quirk, H., Stevens, C. J., Bol, R., Bardgett, R.D. (2012). Extensive management promotes plant and microbial nitrogen retention in temperate grassland. *PLoS One*, **7**, e51201. doi:10.1371/journal.pone.0051201.

Eddy, A., Welch, D., Rawes, M. (1968). The Vegetation of the Moor House National Nature Reserve in the northern Pennines England. *Vegetatio,* **16**, 239-284. https://doi.org/10.1007/BF00257019.

Ghorbani, J., Le Duc, M.G., McAllister, H.A., Pakeman, R.J., Marrs, R. H. (2006). Effects of the litter layer of *Pteridium aquilinum* on seed dynamics under experimental restoration. *Applied Vegetation Science*, **9**, 127–136. https://doi.org/10.1111/j.1654-109X.2006.tb00662.x

Harper, J.L. (1977). *Population Biology of Plants*. Academic Press, London, UK.

Hester, A.J., Gimingham, C.H., Miles, J. (1991). Succession from heather moorland to birch woodland. 3. Seed availability, germination and early growth. *Journal of Ecology*, 79, 329-344. DOI: 10.2307/2260716

Hutchings, M.J., de Kroon, H. (1994). Foraging in Plants: the Role of Morphological Plasticity in Resource Acquisition. *Advances in Ecological Research*, **25**, 159-238. https://doi.org/10.1016/S0065-2504(08)60215-9.

Humphrey, J.W., Coombs, E.L. (1997). Effects of forest management on understorey vegetation in a *Pinus sylvestris* L. Plantation in NE Scotland, *Botanical Journal of Scotland*, **49**, 479-488, DOI: 10.1080/03746609708684893.

Korsman, T., Renberg, I., Dåbak, K. E., Nilsson, M.B. (2001). Near infrared spectrometry (Nirs) in palaeolimnology. In *Tracking environmental change using lake sediments*. Eds. W.M. Last and J.P. Smol. Kluwer Academic Publishers, Dordrecht, pp 299–317.

Lambers, H. & Poorter, H. (1992). Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in Ecological Research* 23, 188-242. **DOI:** 10.1016/S0065-2504(08)60148-8.

Langseth, W., Torgersen, T., Kolsaker, P., Rømming, C., Jantsch, T.G., Mantle, P.G., Pearce, J., Gibson, S.E., Goicochea, M.G., Flåøyen, A. (1999). Isolation and characterization of 3-methoxy-2(5H)-furanone as the principal nephrotoxin from *Narthecium ossifragum* (L.) Huds. *Natural Toxins*, **7**, 111-118. https://doi.org/10.1002/(SICI)1522-7189(199905/06)7:3<111::AID-NT48>3.0.CO;2-F.

Lee, H., Alday, J.G., Rosenburgh, A., Harris, M., McAllister, H., Marrs, R.H. (2013). Change in propagule banks during prescribed burning: a tale of two contrasting moorlands. Biological Conservation*,* **165**, 187–197. https://doi.org/10.1016/j.biocon.2013.05.023.

Linabury, M.C., Turley, N.E., Brudvig, L.A. 2019. Insects remove more seeds than mammals in first-year prairie restorations. *Restoration Ecology*, https://doi.org/10.1111/rec.13004

Lowday, J. E., Marrs, R. H. (1992). Control of bracken and the restoration of heathland. III. Bracken litter disturbance and heathland restoration. *Journal of Applied Ecology*, **29**, 212–217. DOI: 10.2307/2404363.

McGovern, S.T., Evans, C.D., Dennis, P., Walmsley, C.A., McDonald M.A. (2011). Identifying drivers of species compositional change in a semi-natural upland grassland over a 40-year period. *Journal of Vegetation Science*, **22**, 346–356. DOI: 10.1111/j.1654-1103.2011.01256.x.

Marrs, R.H., Rawes, M. Robinson, J.S., Poppitt, S.D. (1986). *Long- term studies of vegetation change at Moor House NNR: guide to recording methods and database.* (Merlewood R&D Paper 109). Institute of Terrestrial Ecology, Grange-over-Sands, UK.

Marrs, R.H., Sánchez, R., Connor, L., Blackbird S., Rasa, J., Rose, R.J. (2018). Effects of removing sheep grazing on soil chemistry, plant nutrition and forage digestibility: lessons for rewilding the British uplands. *Annals of Applied Biology*, **173**, 294–301. DOI:10.1111/aab.1246.

Massey, F.P., Massey, K., Ennos, A.R., Hartley, S.E. 2009. Impacts of silica-based defences in grasses on the feeding preferences of sheep. Ba*sic & Applied Ecology*, **10**, 622-630. DOI: 10.1016/j.baae.2009.04.004.

Merckx, T., Pereira, H.M. (2015). Reshaping agri-environmental subsidies: From marginal farming to large-scale rewilding. *Basic & Applied Ecology*, **16**, 95-103. DOI: 10.1016/j.baae.2014.12.003.

Miles, J. (1974). Experimental establishment of new species from seed in Callunetum in north-east Scotland. *Journal of Ecology*, **62**, 527–555. DOI: 10.2307/2258997.

Milligan, A.L., Putwain, P.D., Cox, E.S., Ghorbani, J., Le Duc, M.G., Marrs, R.H. (2004). Developing an integrated land management strategy for the restoration of moorland vegetation on *Molinia caerulea*-dominated vegetation for conservation purposes in upland Britain. *Biological Conservation*, **119**, 371–385. https://doi.org/10.1016/j.biocon.2003.12.002.

Milligan, G., Rose, R.J., Marrs, R.H. (2016). Winners and losers in a long-term study of vegetation change at Moor House NNR: effects of sheep-grazing and its removal on British upland vegetation. *Ecological Indicators*, **68**, 89–101**.** http://dx.doi.org/10.1016/j.ecolind.2015.10.053.

Milligan, G., Rose, R.J., O'Reilly, J., Marrs, R.H. (2018). Effects of rotational prescribed burning and sheep grazing on moorland plant communities: Results from a 60-year intervention experiment. *Land Degradation & Development,* **29**: 1397–1412. https://doi.org/10.1002/ldr.2953.

Mitchell, R.J., Rose, R.J., Palmer, S.C.F. (2008). Restoration of *Calluna vulgaris* on grass-dominated moorlands: The importance of disturbance, grazing and seeding. *Biological Conservation*, **141** 2100-2111. DOI: 10.1016/j.biocon.2008.06.006. **DOI:** 10.1016/j.biocon.2008.06.006.

Mladkova, P., Mladek, J., Hejduk, S., Hejcman, M., Pakeman, R.J. (2018). Calcium plus magnesium indicates digestibility: the significance of the second major axis of plant chemical variation for ecological processes. *Ecology Letters*, **21**, 885-895. DOI: 10.1111/ele.12956.

Monbiot, G. (2013). *Feral: Searching for enchantment on the frontiers of Rewilding*. Allen Lane, London, UK.

Monteith, D., Henrys, P., Banin, L., Smith, R., Morecroft, M., Scott, T., Andrews, C., Beaumont, D., Benham, S., Bowmaker, V., Corbett, S., Dick, J., Dodd, B., Dodd, N., McKenna, C., McMillan, S.,

Pallet, D., Pereira, M, Poskitt, J., Rennie, S., Rose, R., Schäfer, S., Sherrin, L., Tang, S., Turner, A., Watson H. (2016). Trends and variability in weather and atmospheric deposition at UK Environmental Change Network sites (1993–2012). *Ecological Indicators,* **68**, 21–35. https://doi.org/10.1016/j.ecolind.2016.01.061.

Moise, E.R.D., McNeil, J.N., Hartley, S.E., Henry, H.A.L. 2019. Plant silicon effects on insect feeding dynamics are influenced by plant nitrogen availability. *Entomologia Experimentalis et Applicata*, **167,** 91-97. DOI: 10.1111/eea.12750.

Nakagawa, S., Cuthill, I.C. (2007). Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews*, **82**, 591-605. DOI: 10.1111/j.1469-185X.2007.00027.x.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R. O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagne H. 2019. Package 'vegan' Community Ecology Package Version 2.5-5, 2019-05-08. [accessed 1/10/2019].

Poe, N., Stuble, K.L., Souza, L. (2019). Small mammal herbivores mediate the effects of soil nitrogen and invertebrate herbivores on grassland diversity. *Ecology & Evolution*, **9**, 3577-3587. DOI: 10.1002/ece3.4991.

R Core Team (2017). *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. URL https://www.R-project.org/. [accessed 1/7/2017].

Rawes, M., Welch, D. (1969). Upland productivity of vegetation and sheep at Moor House National Nature Reserves, Westmorland, England. *Oikos Supplementum,* **11**, 1-69.

Rodwell, J. ed. (1991). *British plant communities. Vol. 2. Mires and heaths*. CUP, Cambridge, UK.

Rodwell, J. ed. (1992). *British plant communities. Vol. 3. Grasslands and montane* communities. CUP, Cambridge, UK.

Rose R., Monteith, D.T., Henrys, P., Smart, S., Wood, C., Morecroft, M., Andrews C., Beaumont, D., Benhan, S., Bowmaker, V., Corbett, S., Dick, J., Dodd, B., Dodd, N., Flexen, M., McKenna, C., McMillan, S., Pallett, D., Rennie, S., Schafer, S., Scott, T., Sherrin, L., Turner, A., Watson, H. (2016). Evidence for increases in vegetation species richness across the UK Environmental Change Network sites resulting from changes in air pollution and weather patterns. *Ecological. Indicators* **68**, 52–62. https://doi.org/10.1016/j.ecolind.2016.01.005.

Smart, S.M, Bunce, R.G.H., Marrs, R., Le Duc, M, Firbank, L.G., Maskell, L.C., Scott, W.A., Thompson, K., Walker, K.J. (2005). Large-scale changes in the abundance of common higher plant species across Britain between 1978, 1990 and 1998 as a consequence of human activity: Tests of hypothesised changes in trait presentation. *Biological Conservation*, **124**, 355-371. https://doi.org/10.1016/j.biocon.2004.12.013.

Smart, S.M., Thompson, K., Marrs, R.H., Le Duc, M.G., Maskell, L.C., Firbank, L.G. (2006). Biodiversity loss and biotic homogenization across human-modified ecosystems. *Proceedings of the Royal Society B*, **273**, 2659-2665. https://doi.org/10.1098/rspb.2006.3630.

Smith, R., Shiel, R. S., Bardgett, R. D., Millward, D., Corkhill, P., Rolph, G., Hobbs P. J., Peacock, S. (2003). Soil microbial community, fertility, vegetation and diversity as targets in the restoration management of a meadow grassland. *Journal of Applied Ecology,* **40**, 51–64. doi:10.1046/j.1365-2664.2003.00780.x.

Soulé, M., Noss, R. (1998). Rewilding and biodiversity: Complementary goals for continental conservation. *Wild Earth*, **8**, 19–23.

Stace, C.A. (2019). *New flora of the British Isles, 4th edn*. C & M Floristics, Middlewood Green, Suffolk. UK.

Stewart, M.J. (2010). Does the past matter in Scottish woodland restoration? In: *Restoration and History: the search for a useable environmental past*. edited by M. Hall., pp. 63-73. Routledge, London.

Thompson, K., Parkinson, J.A., Band, S.R., Spencer, R.E. (1997). A comparative study of leaf nutrient concentrations in a regional herbaceous flora. *New Phytologist*, **136**, 679-689. DOI: 10.1046/j.1469-8137.1997.00787.x.

Toogood, M. (1995). Representing ecology and the Highland Tradition. *Area*, **27**, 102-109. https://www.jstor.org/stable/20003526.
van Soest, P.J. (1994). *Nutritional Ecology of the Ruminant.* Cornell University Press. Ithaca, NY.
White, P.J., Broadley, M.R., El-Serehy, H.A., George, T.S., Neugebauer, K. (2018). Linear relationships between shoot magnesium and calcium concentrations among angiosperm species are associated with cell wall chemistry. *Annals of Botany*, **122**, 221-226. DOI: 10.1093/aob/mcy062.

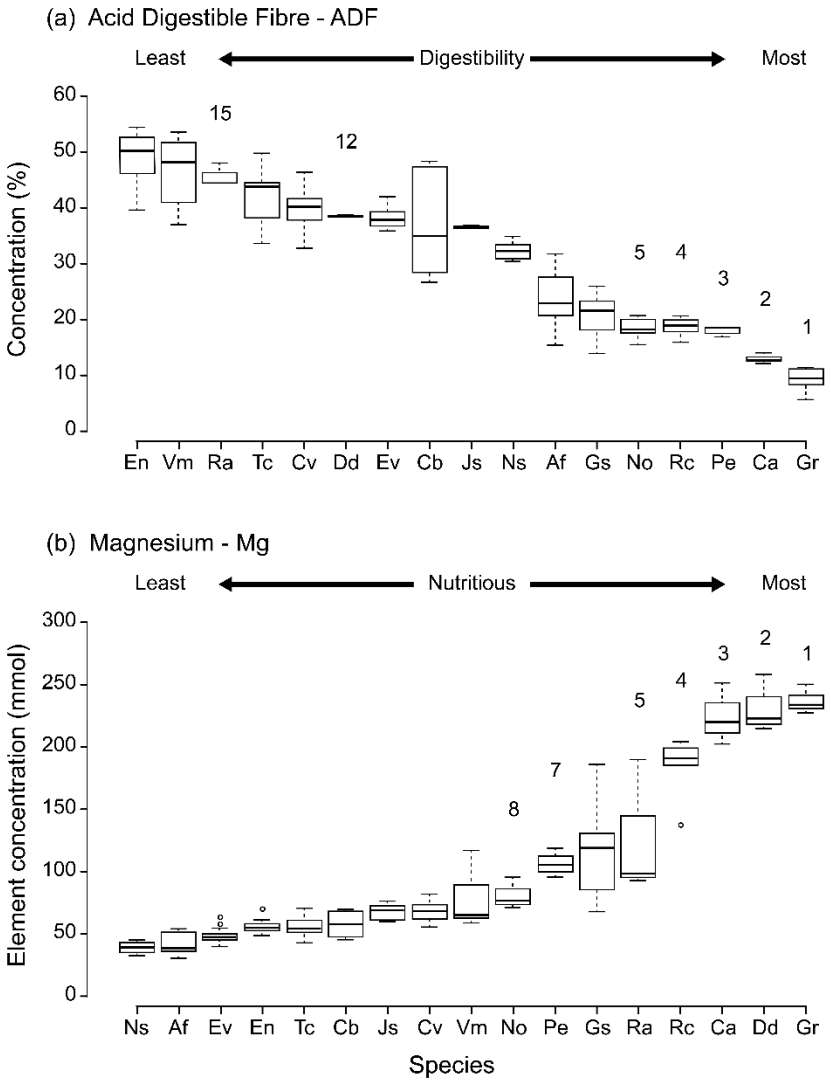


Fig. 1. Two example boxplots illustrating the two types of relationships detected in a study of the relative differences in leaf properties of range of species in the Moor House grazing experiments: (a) where the lowest values have the least nutritional value (Acid Digestible fibre, ADF) and (b) where the largest values have the greatest nutritional value (Mg concentration). Species are ranked via effect size relative to the intercept species (species at the left hand end of axis 1, see Tables S4-S6). The rank of the seven focal species (Table 1) are also illustrated. Species codes: Af = *Avellana flexuosa*, Cv = *Calluna vulgaris*, Cb = *Carex bigelowii*, Ca = *Chamaenerion angustifolium*, Dd = *Dryopteris dilatata*, En = *Empetrum nigrum*, Ev = *Eriophorum vaginatum*, Gs = *Galium saxatile*, Gr = *Geum rivale*, Js = *Juncus squarrosus*, Ns = *Nardus stricta*, No = *Narthecium ossifragum*, Pe = *Potentilla erecta*, Rc = *Rubus chamaemorus*, Ra = *Rumex acetosa*, Tc = *Trichophorum cespitosum*, Vm = *Vaccinium myrtillus*.

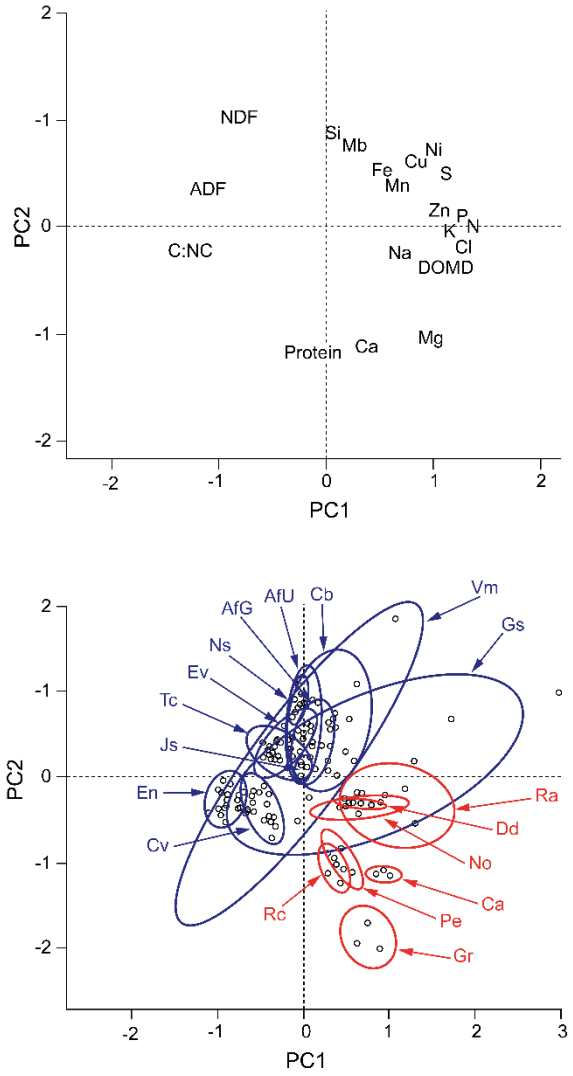


Fig. 2. Biplots from the Principal Components analysis of leaf properties of a range of common (blue) and focal (red) species from the Moor House grazing experiments: (a) plot of leaf property variables, (b) plot of samples overlain with standard deviational ellipses (95%CL) for each species sampled. Species codes: AfU/G = *Avellana flexuosa* Ungrazed/Grazed Cv = *Calluna vulgaris*, Cb = *Carex bigelowii*, Ca = *Chamaenerion angustifolium*, Dd = *Dryopteris dilatata*, En = *Empetrum nigrum*, Ev = *Eriophorum vaginatum*, Gs = *Galium saxatile*, Gr = *Geum rivale*, Js = *Juncus squarrosus*, Ns = *Nardus stricta*, No = *Narthecium ossifragum*, Pe = *Potentilla erecta*, Rc = *Rubus chamaemorus*, Ra = *Rumex acetosa*, Tc = *Trichophorum cespitosum*, Vm = *Vaccinium myrtillus*.

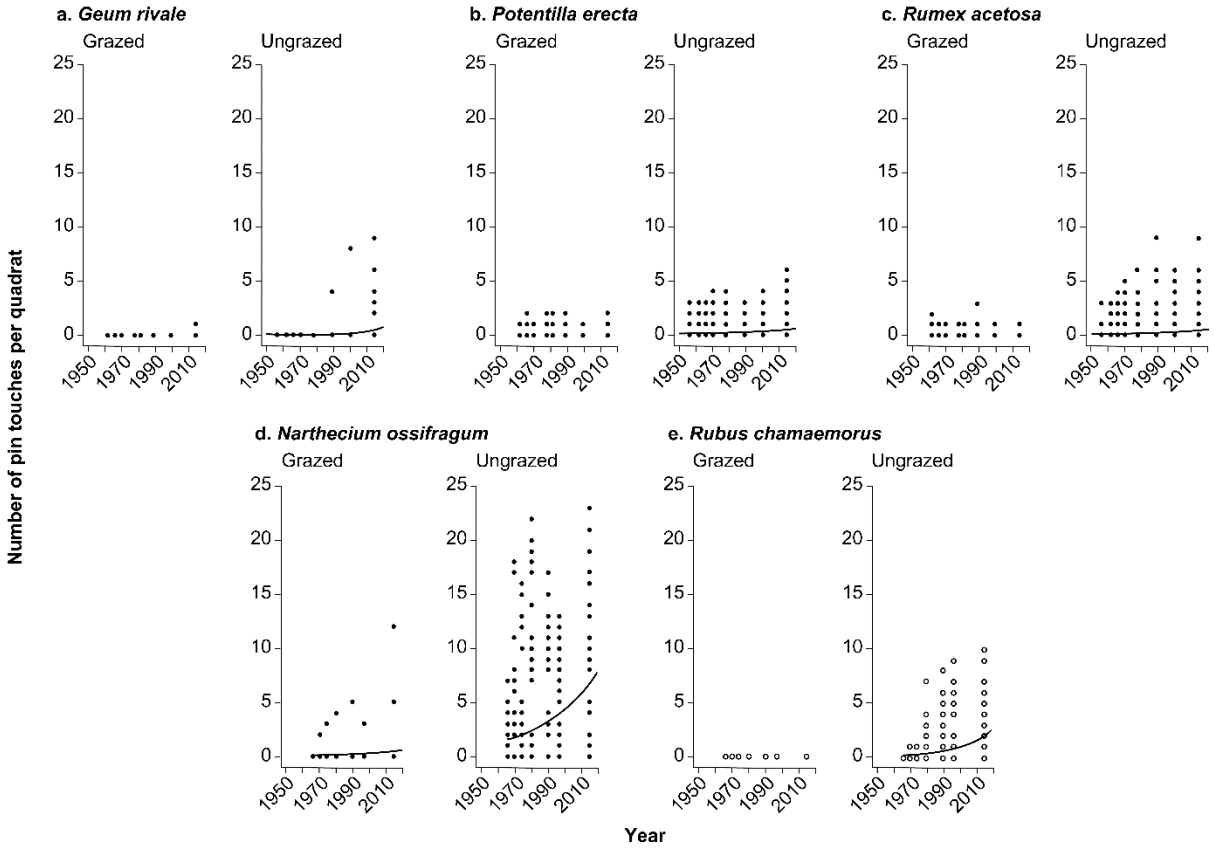


Fig. 3. Change in the abundance of the seven focal species in both grazed and ungrazed plots at Moor House National Nature Reserve in northern England; data are derived from pin quadrat touches. Plotted lines are fitted significant relationships from a Generalized Linear Model; if no line is present a significant relationship could not be fitted; statistical properties of the fitted relationships are presented in Table S8.

Table 1. Summary of the ranks of the seven focal species found in ungrazed plots at Moor House NNR with respect to a range of macro- and micro-nutrient concentrations along with measures of digestibility, palatability and decomposability. The ranks have been derived from glm modelling and subsequent interpretation of boxplots (Fig. 1, Figs. S.1-S.4). The shaded data illustrates species that are in the top 7 with respect to nutritional value (n= 17, except * where n=18) and values in bold type indicate a significant difference (P<0.05) from the intercept (Tables S3-S6). Summary results of a glm to test for differences between focal (F) and common (C) species groups are also presented (full results in Table S7); ns = not significant (P>0.10).

Variable group	Variable	*Chamaenerion angustifolium*	*Dryopteris dilatata*	*Rumex acetosa*	*Narthecium ossifragum*	*Geum rivale*	*Potentilla erecta*	*Rubus chamaemorus*	Focal *versus* Common
Macro-nutrients	Carbon -C	**5**	**7**	**2**	**8**	**1**	**4**	**10**	F<C, P<0.0001
	Nitrogen -N	**3**	**5**	**1**	**2**	**7**	**8**	**10**	F>C, P<0.0001
	Phosphorus - P	**1**	**3**	**2**	**13**	**8**	**6**	**15**	F>C, P<0.0001
	Potassium - K	**7**	**3**	**1**	**10**	**4**	**5**	**12**	F>C, P<0.0001
	Sodium - Na	**6**	**5**	**1**	**2**	16	**4**	**11**	F>C, P<0.0001
	Magnesium - Mg	**3**	**2**	**5**	**8**	**1**	**7**	**4**	F>C, P<0.0001
	Calcium – Ca*	**7**	**9**	**10**	**8**	**1**	**2**	**4**	F>C, P <0.0001
Micro-nutrients	Chlorine – Cl	**2**	**3**	**4**	**1**	**5**	**12**	**7**	F>C, P<0.0001
	Sulphur – S	**7**	**4**	**1**	**2**	**9**	**10**	16	F>C, P<0.10
	Manganese – Mn*	**3**	**2**	**6**	**7**	16	**8**	17	F>C, P<0.0001
	Iron – Fe*	16	5	3	9	15	12	4	F<C, ns
	Copper - Cu	**5**	3	7	17	10	15	16	F<C, ns
	Zinc - Zn	**7**	**3**	**13**	**9**	**11**	**8**	**2**	F>C, P<0.01
	Nickel - Ni	15	**3**	**6**	13	10	11	16	F<C, ns
	Molybdenum - Mb	16	**11**	14	**7**	17	15	**8**	F<C, P<0.001
Digestibility	ADF	**2**	**12**	15	**5**	**1**	**3**	**4**	F<C, P<0.0001
	NDF	nd	**8**	**7**	**6**	**2**	**4**	**1**	F<C, P<0.0001
	DOMD	**2**	**12**	15	**5**	**1**	**3**	**4**	F>C, P<0.0001
	Protein	**3**	**5**	**1**	**2**	**7**	**8**	**10**	F>C, P<0.0001
Palatability	Silicon – Si	**2**	**3**	**5**	**1**	**7**	**10**	**8**	F<C, P<0.0001
Decomposability	C:N ratio	**2**	**4**	**1**	**3**	**5**	**7**	**8**	F<C, P<0.0001

Table S1 Description of the seven monitored sheep-grazing exclosures at Moor House NNR in north-west England (data abstracted from Milligan *et al.*, 2016).

Site Name	Plant community type – Dietary fibre analysis	Site code	British National Grid reference	Elevation (m)	Year established	Vegetation type according to (Eddy *et al.*, 1969)	NVC type according to Milligan *et al.* (2016). (Mean Goodness of fit)	NVC description	Total area of pure stands of the vegetation types on the Moor House reserve (ha)	**Sheep Grazing Density (sheep ha^{-1})
Bog Hill	Bog	BH	NY 76789 32869	550	1953	*Calluna-Eriophorum*	M19 (68%)	*Calluna vulgaris-Eriophorum vaginatum* blanket mire	1169	nd
Silverband	Bog	SB	NY 71059 30975	690	1966	Eriophoretum (eroding)	M20b (71%)	*Eriophorum vaginatum* blanket and raised mire: *Calluna vulgaris-Cladonia* spp. sub-community	323	0.25
Troutbeck Head	Bog	TB	NY 72236 31760	690	1966	Eriophoretum	M20b (73%)	*As above*	419	0.5
Cottage Hill	*Juncus/Nardus*	CH	NY 75801 33641	550	1967	*Juncus squarrosus* grassland	U6b (61%)	*Juncus squarrosus-Festuca ovina* grassland: *Carex nigra-Calypogeia trichomanis* sub-community	373	1.4
River Tees	*Juncus/Nardus*	RT	NY 74796 34485	550	1967	*Nardus stricta* grassland	U5 (73%)	*Nardus stricta-Galium saxatile* grassland	416	2.8
Little Dun Fell	Grass	LDF	NY 70475 33104	830	1954	*Festucetum*	H19a (63%)	As above	-	5.8
Knock Fell	Grass	KF	NY 71794 31267	750	1955	Limestone Agrosto-Festucetum	CG10 (55%)	*Festuca ovina-Agrostis capillaris-Thymus praecox* grassland	125	5.8

*The total area of these communities makes up 3019 ha, i.e. 79% of the reserve area of 3842 ha, the remaining vegetation comprised predominantly re-colonising peatland, Sandstone scree and mosaics of the above vegetation classes (Eddy *et al.*, 1969).

**Sheep grazing density was determined by dropping volume measurement (Rawes and Welch 1969); data were not available for Bog Hill.

Table S2. Comparison of the chemical composition of common species growing in grazed and ungrazed plots at Moor House NNR, all the significant differences (P<0.01) are shown. Mean values (±SE) of transformed data are presented along with the back-transforms and significance assessed either through analysis of variance or Welch's t-test.

Species	Variable	Transform (Units)	Grazed	Ungrazed	$F_{1,13}$	Significance
Avellana flexuosa	Ca	$\log_e(x)$	3.849±0.991	3.027±0.068	50.27	P<0.001
		(mmol)	46.97	20.64		
Avellana flexuosa	Fe	$\log_e(x)$	-2.106±0.174	-2.807±0.074	17.54	P<0.01
		(mg g^{-1})	0.12	0.06		
Avellana flexuosa	Mn	$\log_e(x)$	6.385±0.041	5.781±0.099	17.91	P<0.001
		(µg g^{-1})	593.2	324.2		

Table S.3. Statistical properties of the glm analysis of macro-nutrient concentrations of plant species sampled in the grazing experiments at Moor House NNR; (a) Carbon, (b) Nitrogen, (c) Phosphorus, (d) Potassium, (e) Sodium and (f) Magnesium and (g) Calcium. The intercept species is shaded and the reduction in deviance (%), reduction in AIC, probability and Significance (Sign) are presented. Sign codes: - = P > 0.10, + = P< 0.10, * = P <0.05, ** = P<0.01, *** = P < 0.001. Species codes: Af = *Avellana flexuosa*, Cv = *Calluna vulgaris*, Cb = *Carex bigelowii*, Ca = *Chamaenerion angustifolium*, Dd = *Dryopteris dilatata*, En = *Empetrum nigrum*, Ev = *Eriophorum vaginatum*, Gs = *Galium saxatile*, Gr = *Geum rivale*, Js = *Juncus squarrosus*, Ns = *Nardus stricta*, No = *Narthecium ossifragum*, Pe = *Potentilla erecta*, Rc = *Rubus chamaemorus*, Ra = *Rumex acetosa*, Tc = *Trichophorum cespitosum*, Vm = *Vaccinium myrtillus*.

(a)

C-Carbon	Species	Estimate	SE	t	P	Sign
Statistics	En	10.5608	0.0027	3877.95	<0.0001	***
ΔDev=96.3%	Cv	-0.0196	0.0040	-4.85	<0.0001	***
ΔAIC=431.1	Vm	-0.0639	0.0047	-13.55	<0.0001	***
	Tc	-0.1009	0.0047	-21.38	<0.0001	***
	Js	-0.1079	0.0072	-14.97	<0.0001	***
	Ev	-0.1114	0.0037	-30.01	<0.0001	***
	Cb	-0.1202	0.0054	-22.08	<0.0001	***
	Rc	-0.1236	0.0054	-22.69	<0.0001	***
	Gs	-0.1259	0.0040	-31.17	<0.0001	***
	No	-0.1263	0.0072	-17.53	<0.0001	***
	Dd	-0.1411	0.0072	-19.58	<0.0001	***
	Af	-0.1459	0.0040	-36.12	<0.0001	***
	Ca	-0.1499	0.0072	-20.81	<0.0001	***
	Pe	-0.1548	0.0072	-21.49	<0.0001	***
	Ns	-0.1563	0.0054	-28.69	<0.0001	***
	Ra	-0.1858	0.0072	-25.79	<0.0001	***
	Gr	-0.1862	0.0072	-25.84	<0.0001	***

(b)

N-Nitrogen	Species	Estimate	SE	t	P	Sign
Statistics	En	6.7443	0.0257	262.17	<0.0001	***
ΔDev=87.9%	Cv	0.2306	0.0382	6.05	<0.0001	***
ΔAIC=266.2	Ns	0.4268	0.0515	8.30	<0.0001	***
	Tc	0.4553	0.0446	10.22	<0.0001	***
	Af	0.4624	0.0382	12.12	<0.0001	***
	Js	0.4627	0.0681	6.80	<0.0001	***
	Ev	0.5214	0.0351	14.87	<0.0001	***
	Rc	0.5226	0.0515	10.16	<0.0001	***
	Vm	0.5620	0.0446	12.61	<0.0001	***
	Pe	0.6599	0.0681	9.70	<0.0001	***
	Gr	0.6961	0.0681	10.23	<0.0001	***
	Gs	0.7077	0.0382	18.55	<0.0001	***
	Dd	0.7593	0.0681	11.16	<0.0001	***
	Cb	0.8916	0.0515	17.33	<0.0001	***
	Ca	1.0014	0.0681	14.71	<0.0001	***
	No	1.0148	0.0681	14.91	<0.0001	***
	Ra	1.2189	0.0681	17.91	<0.0001	***

(c)

P-Phosphorus	Species	Estimate	SE	t	P	Sign
Statistics	En	3.6292	0.0527	68.81	<0.0001	***
ΔDev=79.3%	Cv	0.1852	0.0782	2.37	<0.0001	***
ΔAIC=190.2	Rc	0.2456	0.1055	2.33	0.0215	*
	Tc	0.3091	0.0914	3.38	0.0010	***
	No	0.4530	0.1395	3.25	0.0015	**
	Ns	0.5165	0.1055	4.90	<0.0001	***
	Ev	0.6531	0.0719	9.09	<0.0001	***
	Js	0.6681	0.1395	4.79	<0.0001	***
	Af	0.7233	0.0782	9.25	<0.0001	***
	Gr	0.7589	0.1395	5.44	<0.0001	***
	Vm	0.7590	0.0914	8.31	<0.0001	***
	Pe	0.8449	0.1395	6.06	<0.0001	***
	Cb	1.1255	0.1055	10.67	<0.0001	***
	Gs	1.1785	0.0782	15.07	<0.0001	***
	Dd	1.2587	0.1395	9.02	<0.0001	***
	Ra	1.4204	0.1395	10.18	<0.0001	***
	Ca	1.4897	0.1395	10.68	<0.0001	***

(d)

K-Potassium	Species	Estimate	SE	t	P	Sign
Statistics	En	4.2915	0.0466	92.01	<0.0001	***
ΔDev=89.0%	Cv	0.1811	0.0692	2.62	0.0100	**
ΔAIC=278.8	Vm	0.3806	0.0808	4.71	<0.0001	***
	Tc	0.4632	0.0808	5.73	<0.0001	***
	Ev	0.5696	0.0636	8.96	<0.0001	***
	Rc	1.0057	0.0933	10.78	<0.0001	***
	Ns	1.0083	0.0933	10.81	<0.0001	***
	No	1.0086	0.1234	8.17	<0.0001	***
	Af	1.1460	0.0692	16.57	<0.0001	***
	Js	1.2444	0.1234	10.09	<0.0001	***
	Ca	1.2691	0.1234	10.28	<0.0001	***
	Gs	1.2736	0.0692	18.41	<0.0001	***
	Pe	1.2819	0.1234	10.39	<0.0001	***
	Gr	1.3216	0.1234	10.71	<0.0001	***
	Dd	1.3240	0.1234	10.73	<0.0001	***
	Cb	1.3845	0.0933	14.84	<0.0001	***
	Ra	2.3140	0.1234	18.75	<0.0001	***

(e)

Na-Sodium	Species	Estimate	SE	t	P	Sign
Statistics	En	2.4369	0.0730	33.36	<0.0001	***
ΔDev=74.6%	Gr	0.3614	0.1933	1.87	0.0639	+
ΔAIC=161.1	Vm	0.3728	0.1265	2.95	0.0038	**
	Ev	0.5168	0.0995	5.19	<0.0001	***
	Af	0.5538	0.1083	5.11	<0.0001	***
	Ns	0.7281	0.1461	4.98	<0.0001	***
	Rc	0.7907	0.1461	5.41	<0.0001	***
	Gs	0.8504	0.1083	7.85	<0.0001	***
	Tc	0.9852	0.1265	7.79	<0.0001	***
	Cb	1.0822	0.1461	7.41	<0.0001	***
	Cv	1.1078	0.1083	10.23	<0.0001	***
	Ca	1.1614	0.1933	6.01	<0.0001	***
	Dd	1.4221	0.1933	7.36	<0.0001	***
	Pe	1.5900	0.1933	8.23	<0.0001	***
	Js	1.6309	0.1933	8.44	<0.0001	***
	No	2.0879	0.1933	10.80	<0.0001	***
	Ra	2.2171	0.1933	11.47	<0.0001	***

(f)

Mg-Magnesium	Species	Estimate	SE	t	P	Sign
Statistics	Ns	3.5594	0.0772	46.12	<0.0001	***
ΔDev=89.3%	Af	0.0806	0.0913	0.88	<0.0001	***
ΔAIC=283.7	Ev	0.2485	0.0875	2.84	<0.0001	***
	En	0.3928	0.0891	4.41	<0.0001	***
	Tc	0.3934	0.0997	3.95	<0.0001	***
	Cb	0.4193	0.1092	3.84	<0.0001	***
	Js	0.5725	0.1337	4.28	<0.0001	***
	Cv	0.6014	0.0913	6.59	<0.0001	***
	Vm	0.6922	0.0997	6.95	<0.0001	***
	No	0.7895	0.1337	5.91	<0.0001	***
	Pe	1.0815	0.1337	8.09	<0.0001	***
	Gs	1.1157	0.0913	12.22	<0.0001	***
	Ra	1.2059	0.1337	9.02	<0.0001	***
	Rc	1.6422	0.1092	15.04	<0.0001	***
	Ca	1.8467	0.1337	13.81	<0.0001	***
	Dd	1.8795	0.1337	14.06	<0.0001	***
	Gr	1.9052	0.1337	14.25	<0.0001	***

(g)

Ca-Calcium	Species	Estimate	SE	t	P	Sign
Statistics	Js	2.9681	0.2034	14.60	<0.0001	***
ΔDev=82.0%	Ns	0.0399	0.2491	0.16	0.8729	-
ΔAIC=207.8	Af-U	0.0591	0.2348	0.25	0.8017	-
	Tc	0.4731	0.2348	2.01	0.0461	*
	Ev	0.5559	0.2174	2.56	0.0118	*
	Cb	0.5908	0.2491	2.37	0.0192	*
	Af-G	0.8811	0.2491	3.54	0.0006	***
	Cv	1.2078	0.2228	5.42	<0.0001	***
	Ra	1.2781	0.2876	4.44	<0.0001	***
	Dd	1.4258	0.2876	4.96	<0.0001	***
	No	1.4960	0.2876	5.20	<0.0001	***
	Ca	1.5070	0.2876	5.24	<0.0001	***
	Gs	1.5190	0.2228	6.82	<0.0001	***
	En	1.5229	0.2197	6.93	<0.0001	***
	Rc	1.8744	0.2491	7.53	<0.0001	***
	Vm	1.9537	0.2348	8.32	<0.0001	***
	Pe	2.6143	0.2876	9.09	<0.0001	***
	Gr	3.2132	0.2876	11.17	<0.0001	***

Table S4. Statistical properties of the glm analysis of micro-nutrient concentrations of plant species sampled in the grazing experiments at Moor House NNR; (a) Carbon, (b) Nitrogen, (c) Phosphorus, (d) Potassium, (e) Sodium and (f) Magnesium and (g) Calcium. The intercept species is shaded and the reduction in deviance (%), reduction in AIC, probability and Significance (Sign) are presented. Sign codes: - = P > 0.10, + = P< 0.10, * = P <0.05, ** = P<0.01, *** = P < 0.001. Species codes: Af = *Avellana flexuosa*, Cv = *Calluna vulgaris*, Cb = *Carex bigelowii*, Ca = *Chamaenerion angustifolium*, Dd = *Dryopteris dilatata*, En = *Empetrum nigrum*, Ev = *Eriophorum vaginatum*, Gs = *Galium saxatile*, Gr = *Geum rivale*, Js = *Juncus squarrosus*, Ns = *Nardus stricta*, No = *Narthecium ossifragum*, Pe = *Potentilla erecta*, Rc = *Rubus chamaemorus*, Ra = *Rumex acetosa*, Tc = *Trichophorum cespitosum*, Vm = *Vaccinium myrtillus*.

(a)

S-Sulphur	Species	Estimate	SE	t	P	Sign
Statistics	En	0.5603	0.0609	9.21	<0.0001	***
ΔDev=48.5%	Rc	0.0182	0.1217	0.15	0.8817	-
ΔAIC=61.5	Js	0.1140	0.1610	0.71	0.4801	-
	Ev	0.1638	0.0829	1.98	0.0505	+
	Cv	0.2059	0.0903	2.28	0.0242	*
	Tc	0.2595	0.1054	2.46	0.0152	*
	Af	0.2912	0.0903	3.23	0.0016	**
	Pe	0.3268	0.1610	2.03	0.0445	*
	Gr	0.3280	0.1610	2.04	0.0438	*
	Ns	0.4017	0.1217	3.30	0.0013	**
	Ca	0.4168	0.1610	2.59	0.0108	*
	Cb	0.4439	0.1217	3.65	0.0004	***
	Vm	0.5638	0.1054	5.35	0.0000	***
	Dd	0.6738	0.1610	4.19	0.0001	***
	Gs	0.6760	0.0903	7.49	0.0000	***
	No	0.7405	0.1610	4.60	0.0000	***
	Ra	0.8985	0.1610	5.58	0.0000	***

(b)

Fe-Iron	Species	Estimate	SE	t	P	Sign
Statistics	Js	-2.9379	0.2088	-14.07	<0.0001	***
ΔDev=23.6%	Ca	0.0532	0.2953	0.18	0.8573	-
ΔAIC=5.9	Gr	0.0848	0.2953	0.29	0.7745	-
	En	0.1161	0.2255	0.52	0.6076	-
	Af-U	0.1312	0.2411	0.54	0.5872	-
	Ns	0.2028	0.2557	0.79	0.4293	-
	Pe	0.2704	0.2953	0.92	0.3616	-
	Vm	0.2716	0.2411	1.13	0.26	-
	Cb	0.2771	0.2557	1.08	0.2807	-
	No	0.2888	0.2953	0.98	0.3299	-
	Ev	0.3260	0.2232	1.46	0.1467	-
	Tc	0.3446	0.2411	1.43	0.1554	-
	Cv	0.4111	0.2287	1.80	0.0747	+
	Dd	0.4428	0.2953	1.50	0.1363	-
	Rc	0.4968	0.2557	1.94	0.0544	+
	Ra	0.5262	0.2953	1.78	0.0773	+
	Gs	0.8022	0.2287	3.51	0.0006	***
	Af-G	0.8315	0.2557	3.25	0.0015	**

(c)

(d)

Cl-Chlorine	Species	Estimate	SE	t	P	Sign
Statistics	En	6.0341	0.1071	56.36	<0.0001	***
ΔDev=83.9%	Ev	0.2273	0.1459	1.56	0.1220	-
2 ΔAIC=25.2	Cv	1.0556	0.1588	6.65	<0.0001	***
	Vm	1.077	0.1854	5.808	<0.0001	***
	Cb	1.2797	0.2141	5.98	<0.0001	***
	Pe	1.8894	0.2833	6.67	<0.0001	***
	Gs	1.9527	0.1588	12.30	<0.0001	***
	Tc	2.0504	0.1854	11.06	<0.0001	***
	Af	2.0622	0.1588	12.99	<0.0001	***
	Ns	2.2643	0.2141	10.58	<0.0001	***
	Rc	2.5338	0.2141	11.83	<0.0001	***
	Js	2.6022	0.2833	9.19	<0.0001	***
	Gr	2.7621	0.2833	9.75	<0.0001	***
	Ra	2.8147	0.2833	9.94	<0.0001	***
	Dd	2.9024	0.2833	10.25	<0.0001	***
	Ca	2.9307	0.2833	10.35	<0.0001	***
	No	3.0876	0.2833	10.90	<0.0001	***

Mn-Manganese	Species	Estimate	SE	t	P	Sign
Statistics	Ev	4.2962	0.1204	35.67	<0.0001	***
ΔDev=70.9%	Rc	0.4581	0.2555	1.79	0.0755	+
ΔAIC=142.1	Gr	0.5253	0.3407	1.54	0.1256	-
	Tc	0.5547	0.2199	2.52	0.0129	*
	Js	0.9177	0.3407	2.69	0.0081	**
	En	0.9558	0.1773	5.39	<0.0001	***
	Ns	1.2322	0.2555	4.82	<0.0001	***
	Cb	1.3183	0.2555	5.16	<0.0001	***
	Cv	1.3678	0.1866	7.33	<0.0001	***
	Af-U	1.4851	0.2199	6.75	<0.0001	***
	Pe	1.5039	0.3407	4.42	<0.0001	***
	No	1.5932	0.3407	4.68	<0.0001	***
	Ra	1.6502	0.3407	4.84	<0.0001	***
	Gs	2.0616	0.1866	11.05	<0.0001	***
	Af-G	2.0893	0.2555	8.18	<0.0001	***
	Ca	2.2860	0.3407	6.71	<0.0001	***
	Dd	2.6329	0.3407	7.73	<0.0001	***
	Vm	2.9708	0.2199	13.51	<0.0001	***

(e)

Ni-Nickel	Species	Estimate	SE	t	P	Sign
Statistics	En	2.2539	0.0642	35.12	<0.0001	***
ΔDev=44.8%	Rc	0.0339	0.1284	0.26	0.7923	-
ΔAIC=51.8	Ca	0.0911	0.1698	0.54	0.5925	-
	Cv	0.1026	0.0952	1.08	0.2832	-
	No	0.1430	0.1698	0.84	0.4014	-
	Js	0.1847	0.1698	1.09	0.2789	-
	Pe	0.2053	0.1698	1.21	0.2290	-
	Gr	0.2717	0.1698	1.60	0.1122	-
	Tc	0.2815	0.1112	2.53	0.0126	*
	Ev	0.2873	0.0875	3.29	0.0013	**
	Cb	0.3818	0.1284	2.97	0.0035	**
	Ra	0.4818	0.1698	2.84	0.0053	**
	Ns	0.4941	0.1284	3.85	0.0002	***
	Af	0.5178	0.0952	5.44	<0.0001	***
	Dd	0.5956	0.1698	3.51	0.0006	***
	Vm	0.6093	0.1112	5.48	<0.0001	***
	Gs	0.7016	0.0952	7.37	<0.0001	***

(f)

Cu-Copper	Species	Estimate	SE	t	P	Sign
Statistics	No	1.7976	0.1475	12.19	<0.0001	***
ΔDev=39.7%	Rc	0.1072	0.1806	0.59	0.5539	-
ΔAIC=39.4	Pe	0.1286	0.2086	0.62	0.5386	-
	Js	0.1715	0.2086	0.82	0.4124	-
	En	0.1847	0.1593	1.16	0.2484	-
	Ev	0.2111	0.1577	1.34	0.1830	-
	Af	0.2153	0.1616	1.33	0.1851	-
	Gr	0.2330	0.2086	1.12	0.2661	-
	Ns	0.2692	0.1806	1.49	0.1386	-
	Tc	0.2769	0.1703	1.63	0.1065	-
	Ra	0.3195	0.2086	1.53	0.1281	-
	Cv	0.3311	0.1616	2.05	0.0425	*
	Ca	0.4878	0.2086	2.34	0.0210	*
	Vm	0.5043	0.1703	2.96	0.0037	**
	Dd	0.5207	0.2086	2.50	0.0139	*
	Gs	0.5406	0.1616	3.35	0.0011	**
	Cb	0.9706	0.1806	5.37	<0.0001	***

(g)

Zinc	Species	Estimate	SE	t	P	Sign
Statistics	En	2.9888	0.0606	49.35	<0.0001	***
ΔDev=88.9%	Cv	0.1994	0.0898	2.22	0.0283	*
ΔAIC=278.2	Af	0.5395	0.0898	6.01	<0.0001	***
	Cb	0.7559	0.1211	6.24	<0.0001	***
	Ra	0.7810	0.1603	4.87	<0.0001	***
	Tc	0.8063	0.1049	7.69	<0.0001	***
	Gr	0.8644	0.1603	5.39	<0.0001	***
	Vm	0.9042	0.1049	8.62	<0.0001	***
	No	1.1122	0.1603	6.94	<0.0001	***
	Pe	1.1266	0.1603	7.03	<0.0001	***
	Ca	1.1978	0.1603	7.48	<0.0001	***
	Js	1.2225	0.1603	7.63	<0.0001	***
	Ns	1.2461	0.1211	10.29	<0.0001	***
	Ev	1.5255	0.0825	18.48	<0.0001	***
	Dd	1.7973	0.1603	11.22	<0.0001	***
	Rc	1.9181	0.1211	15.83	<0.0001	***
	Gs	2.1682	0.0898	24.14	<0.0001	***

(h)

Molybdenum	Species	Estimate	SE	t	P	Sign
Statistics	Gr	-4.6052	0.9144	-5.04	<0.0001	***
ΔDev=43.6%	Ca	1.3040	1.2932	1.01	0.3152	
ΔAIC=48.7	Pe	1.3648	1.2932	1.06	0.2933	
	Ra	1.4999	1.2932	1.16	0.2483	
	Vm	1.5597	1.0559	1.48	0.1422	
	En	2.8484	0.9877	2.88	0.0046	**
	Dd	3.1627	1.2932	2.45	0.0159	*
	Cv	3.9729	1.0017	3.97	0.0001	***
	Tc	4.1689	1.0559	3.95	0.0001	***
	Rc	4.1890	1.1199	3.74	0.0003	***
	No	4.5471	1.2932	3.52	0.0006	***
	Ev	4.7318	0.9776	4.84	<0.0001	***
	Ns	4.8039	1.1199	4.29	<0.0001	***
	Js	4.8740	1.2932	3.77	0.0003	***
	Gs	4.9055	1.0017	4.90	<0.0001	***
	Af	4.9488	1.0017	4.94	<0.0001	***
	Cb	5.2311	1.1199	4.67	<0.0001	***

Table S.5. Statistical properties of the glm analysis of digestibility variables of plant species sampled in the grazing experiments at Moor House NNR; (a) Carbon, (b) Nitrogen, (c) Phosphorus, (d) Potassium, (e) Sodium and (f) Magnesium and (g) Calcium. The intercept species is shaded and the reduction in deviance (%), reduction in AIC, probability and Significance (Sign) are presented. Sign codes: - = P > 0.10, + = P< 0.10, * = P <0.05, ** = P<0.01, *** = P < 0.001. Species codes: Af = *Avellana flexuosa*, Cv = *Calluna vulgaris*, Cb = *Carex bigelowii*, Ca = *Chamaenerion angustifolium*, Dd = *Dryopteris dilatata*, En = *Empetrum nigrum*, Ev = *Eriophorum vaginatum*, Gs = *Galium saxatile*, Gr = *Geum rivale*, Js = *Juncus squarrosus*, Ns = *Nardus stricta*, No = *Narthecium ossifragum*, Pe = *Potentilla erecta*, Rc = *Rubus chamaemorus*, Ra = *Rumex acetosa*, Tc = *Trichophorum cespitosum*, Vm = *Vaccinium myrtillus*.

(a)

ADF	Species	Estimate	SE	t	P	Sign
Statistics	En	49.1391	0.9829	50.00	<0.0001	***
ΔDev=89.4	Vm	-2.3638	1.7024	-1.39	0.1670	-
ΔAIC282.3	Ra	-3.6390	2.6004	-1.40	0.1640	-
	Tc	-7.4868	1.7024	-4.40	<0.0001	***
	Cv	-9.6657	1.4578	-6.63	<0.0001	***
	Dd	-10.8531	2.6004	-4.17	<0.0001	***
	Ev	-11.1345	1.3394	-8.31	<0.0001	***
	Cb	-12.6818	1.9658	-6.45	<0.0001	***
	Js	-12.7438	2.6004	-4.90	<0.0001	***
	Ns	-16.9902	1.9658	-8.64	<0.0001	***
	Af	-25.7660	1.4578	-17.67	<0.0001	***
	Gs	-28.9883	1.4860	-19.51	<0.0001	***
	No	-30.7364	2.6004	-11.82	<0.0001	***
	Rc	-30.7580	1.9658	-15.65	<0.0001	***
	Pe	-31.4647	2.6004	-12.10	<0.0001	***
	Ca	-36.5629	2.6004	-14.06	<0.0001	***
	Gr	-40.1334	2.6004	-15.43	<0.0001	***

(b)

NDF	Species	Estimate	SE	t	P	Sign
Statistics	Ns	69.3930	1.8910	37	<0.0001	***
ΔDev=92.7	Tc	-7.7720	2.4420	-3	0.0019	**
ΔAIC=329.2	Ev	-9.6620	2.1450	-5	<0.0001	***
	Af	-12.0650	2.2380	-5	<0.0001	***
	Cb	-12.3390	2.6750	-5	<0.0001	***
	En	-13.5630	2.1840	-6	<0.0001	***
	Vm	-14.1400	2.4420	-6	<0.0001	***
	Js	-19.0900	3.2760	-6	<0.0001	***
	Dd	-21.3020	3.2760	-7	<0.0001	***
	Ra	-28.8450	3.2760	-9	<0.0001	***
	No	-33.3520	3.2760	-10	<0.0001	***
	Cv	-34.4250	2.2380	-15	<0.0001	***
	Pe	-41.7880	3.2760	-13	<0.0001	***
	Gs	-45.0350	2.2610	-20	<0.0001	***
	Gr	-52.8990	3.2760	-16	<0.0001	***
	Rc	-56.1820	2.6750	-21	<0.0001	***

(c)

DOMD	Species	Estimate	SE	t	P	Sign
Statistics	En	47.205	1.022	46.18	<0.0001	***
ΔDev=89.4	Vm	2.458	1.770	1.39	0.167	-
ΔAIC=282.3	Ra	3.785	2.704	1.40	0.164	-
	Tc	7.786	1.770	4.40	<0.0001	***
	Cv	10.052	1.516	6.63	<0.0001	***
	Dd	11.287	2.704	4.17	<0.0001	***
	Ev	11.580	1.393	8.31	<0.0001	***
	Cb	13.189	2.044	6.45	<0.0001	***
	Js	13.254	2.704	4.90	<0.0001	***
	Ns	17.670	2.044	8.64	<0.0001	***
	Af	26.797	1.516	17.67	<0.0001	***
	Gs	30.148	1.545	19.51	<0.0001	***
	No	31.966	2.704	11.82	<0.0001	***
	Rc	31.988	2.044	15.65	<0.0001	***
	Pe	32.723	2.704	12.10	<0.0001	***
	Ca	38.025	2.704	14.06	<0.0001	***
	Gr	41.739	2.704	15.43	<0.0001	***

(d)

Protein	Species	Estimate	SE	t	P	Sign
Statistics	En	0.2554	0.0047	54.64	<0.0001	***
ΔDev=92.7	Cv	0.0319	0.0069	4.60	<0.0001	***
ΔAIC=333.8	Ns	0.0625	0.0093	6.69	<0.0001	***
	Tc	0.0677	0.0081	8.36	<0.0001	***
	Js	0.0686	0.0124	5.55	<0.0001	***
	Af	0.0690	0.0069	9.96	<0.0001	***
	Ev	0.0789	0.0064	12.38	<0.0001	***
	Rc	0.0789	0.0093	8.44	<0.0001	***
	Vm	0.0863	0.0081	10.67	<0.0001	***
	Pe	0.1036	0.0124	8.38	<0.0001	***
	Gr	0.1103	0.0124	8.92	<0.0001	***
	Gs	0.1137	0.0069	16.40	<0.0001	***
	Dd	0.1230	0.0124	9.95	<0.0001	***
	Cb	0.1503	0.0093	16.08	<0.0001	***
	Ca	0.1741	0.0124	14.08	<0.0001	***
	No	0.1779	0.0124	14.39	<0.0001	***
	Ra	0.2280	0.0124	18.44	<0.0001	***

Table S6. Statistical properties of the glm analysis of (a) decomposability and (b) decompsability of plant species sampled in the grazing experiments at Moor House NNR. The intercept species is shaded and the reduction in deviance (%), reduction in AIC, probability and Significance (Sign) are presented. Sign codes: - = P > 0.10, + = P< 0.10, * = P <0.05, ** = P<0.01, *** = P < 0.001. Species codes: Species codes: Af = *Avellana flexuosa*, Cv = *Calluna vulgaris*, Cb = *Carex bigelowii*, Ca = *Chamaenerion angustifolium*, Dd = *Dryopteris dilatata*, En = *Empetrum nigrum*, Ev = *Eriophorum vaginatum*, Gs = *Galium saxatile*, Gr = *Geum rivale*, Js = *Juncus squarrosus*, Ns = *Nardus stricta*, No = *Narthecium ossifragum*, Pe = *Potentilla erecta*, Rc = *Rubus chamaemorus*, Ra = *Rumex acetosa*, Tc = *Trichophorum cespitosum*, Vm = *Vaccinium myrtillus*.

(a)

Silicon	Species	Estimate	SE	t	P	Sign
Statistics	Ns	2.6416	0.2472	10.69	<0.0001	***
ΔDev=72.6	Af	-1.3181	0.2925	-4.51	<0.0001	***
ΔAIC=150.4	Cb	-1.6763	0.3496	-4.80	<0.0001	***
	Ev	-2.5744	0.2803	-9.18	<0.0001	***
	Gs	-2.6012	0.2925	-8.89	<0.0001	***
	Tc	-2.8147	0.3191	-8.82	<0.0001	***
	Cv	-2.9633	0.2925	-10.13	<0.0001	***
	Pe	-3.0055	0.4282	-7.02	<0.0001	***
	Vm	-3.2754	0.3191	-10.26	<0.0001	***
	Rc	-3.3953	0.3496	-9.71	<0.0001	***
	Gr	-3.3984	0.4282	-7.94	<0.0001	***
	Js	-3.4505	0.4282	-8.06	<0.0001	***
	Ra	-3.5019	0.4282	-8.18	<0.0001	***
	En	-3.5417	0.2855	-12.41	<0.0001	***
	Dd	-3.6197	0.4282	-8.45	<0.0001	***
	Ca	-4.1066	0.4282	-9.59	<0.0001	***
	No	-4.2879	0.4282	-10.01	<0.0001	***

(b)

C:N ratio	Species	Estimate	SE	t	P	Sign
Statistics	En	3.9711	0.0261	152.15	<0.0001	***
ΔDev=90.6	Cv	-0.2502	0.0387	-6.46	<0.0001	***
ΔAIC=300.8	Tc	-0.5561	0.0452	-12.30	0.0215	*
	Js	-0.5705	0.0691	-8.26	0.0010	***
	Ns	-0.5830	0.0522	-11.17	0.0015	**
	Af	-0.6083	0.0387	-15.71	<0.0001	***
	Vm	-0.6259	0.0452	-13.85	<0.0001	***
	Ev	-0.6328	0.0356	-17.79	<0.0001	***
	Rc	-0.6462	0.0522	-12.38	<0.0001	***
	Pe	-0.8148	0.0691	-11.80	<0.0001	***
	Gs	-0.8336	0.0387	-21.53	<0.0001	***
	Gr	-0.8823	0.0691	-12.78	<0.0001	***
	Dd	-0.9004	0.0691	-13.04	<0.0001	***
	Cb	-1.0118	0.0522	-19.38	<0.0001	***
	No	-1.1411	0.0691	-16.52	<0.0001	***
	Ca	-1.1513	0.0691	-16.67	<0.0001	***
	Ra	-1.4047	0.0691	-20.34	<0.0001	***

Table S7. Statistical properties of the glm analysis of all variables sampled in the grazing experiments at Moor House NNR testing for differences between the Common *versus* Focal species. The reduction in deviance (%), reduction in AIC, probability and Significance (Sign) are presented. Sign codes: - = P > 0.10, + = P< 0.10, * = P <0.05, ** = P<0.01, *** = P < 0.001.

Variable	Species Group	Estimate	SE	t	P	Sign.	%ΔDeviance	%ΔAIC
C	Common Species (Int)	10.505	0.009	1189.97	<0.0001	***	17.3	24.8
	Focal Species	-0.031	0.006	-5.39	<0.0001	***		
N	Common Species (Int)	6.991	0.045	155.00	<0.0001	***	22.1	33.2
	Focal Species	0.184	0.029	6.28	<0.0001	***		
P	Common Species (Int)	4.062	0.078	52.05	<0.0001	***	4.9	5.1
	Focal Species	0.136	0.051	2.67	0.0085	**		
K	Common Species (Int)	4.616	0.087	53.19	<0.0001	***	19.8	29.1
	Focal Species	0.331	0.056	5.85	<0.0001	***		
Na	Common Species (Int)	2.7664	0.0906	30.55	<0.0001	***	17.9	25.8
	Focal Species	0.3244	0.0589	5.50	<0.0001	***		
Mg	Common Species (Int)	3.493	0.065	53.60	<0.0001	***	52.2	102
	Focal Species	0.522	0.042	12.31	<0.0001	***		
Ca	Common Species (Int)	3.442	0.119	28.89	<0.0001	***	21.6	32.2
	Focal Species	0.479	0.078	6.18	<0.0001	***		
Cl	Common Species (Int)	6.463	0.156	41.53	<0.0001	***	28.3	45
	Focal Species	0.751	0.101	7.42	<0.0001	***		
S	Common Species (Int)	0.781	0.058	13.51	<0.0001	***	2.4	1.4
	Focal Species	0.069	0.038	1.84	0.0683	+		
Mn	Common Species (Int)	5.452	0.168	32.39	<0.0001	***	0.4	1.5
	Focal Species	0.077	0.110	0.71	0.4810	ns		
Fe	Common Species (Int)	-2.569	0.071	-36.40	<0.0001	***	0.1	1.9
	Focal Species	-0.012	0.046	-0.26	0.7920	ns		
Cu	Common Species (Int)	2.179	0.053	41.01	<0.0001	***	1.4	0.1
	Focal Species	-0.048	0.035	-1.38	0.1690	ns		
Zn	Common Species (Int)	3.687	0.122	30.12	<0.0001	***	4.9	5.1
	Focal Species	0.214	0.080	2.68	0.0082	**		
Ni	Common Species (Int)	2.647	0.059	44.71	<0.0001	***	1.4	0.1
	Focal Species	-0.054	0.039	-1.39	0.1660	ns		
Mb	Common Species (Int)	0.340	0.327	1.04	0.3002	ns	9.3	11.8
	Focal Species	-0.804	0.212	-3.79	0.0002	***		
ADF	Common Species (Int)	43.484	1.872	23.23	<0.0001	***	19.7	28.7
	Focal Species	-7.069	1.216	-5.82	<0.0001	***		
NDF	Common Species (Int)	62.948	2.456	25.63	<0.0001	***	27.2	41.4
	Focal Species	-11.687	1.646	-7.10	<0.0001	***		
DOMD	Common Species (Int)	53.087	1.947	27.27	<0.0001	***	19.7	28.7
	Focal Species	7.352	1.264	5.82	<0.0001	***		
Protein	Common Species (Int)	0.287	0.008	36.62	<0.0001	***	24.2	37.2
	Focal Species	0.034	0.005	6.67	<0.0001	***		
C:N	Common Species (Int)	3.669	0.051	71.29	<0.0001	***	22.9	34.7
	Focal Species	-0.215	0.033	-6.43	<0.0001	***		
Si	Common Species (Int)	0.638	0.175	3.64	<0.0001	***	13.4	18.3
	Focal Species	-0.528	0.114	-4.64	<0.0001	***		

Table S8. Properties of the Generalized Linear models of the temporal responses of focal species described in Figure 5.

Species	Grazing Treatment	Parameter	Estimate	Std. Error	z value	Probability	Significance	ΔAIC	ΔDeviance
Geum rivale	Ungrazed	Intercept	-178.388	20.218	-8.823	<0.0001	***	135.16	137.16
		Year	0.088	0.010	8.752	<0.0001	***		
Narthecium ossifragum	Grazed	Intercept	-118.864	20.087	-5.917	<0.0001	***	36.28	38.28
		Year	0.059	0.010	5.833	<0.0001	***		
	Ungrazed	Intercept	-58.963	3.526	-16.720	<0.0001	***	282.4	284.3
		Year	0.030	0.002	17.080	<0.0001	***		
Potentilla erecta	Ungrazed	Intercept	-52.777	7.762	-6.799	<0.0001	***	41.48	43.52
		Year	0.026	0.004	6.615	<0.0001	***		
Rumex acetosa	Ungrazed	Intercept	-89.529	5.579	-16.050	<0.0001	***	281	283
		Year	0.045	0.003	15.980	<0.0001	***		
Rubus chamaemorus	Ungrazed	Intercept	-105.000	8.407	-12.490	<0.0001	***	165.77	167.79
		Year	0.052	0.004	12.480	<0.0001	***		

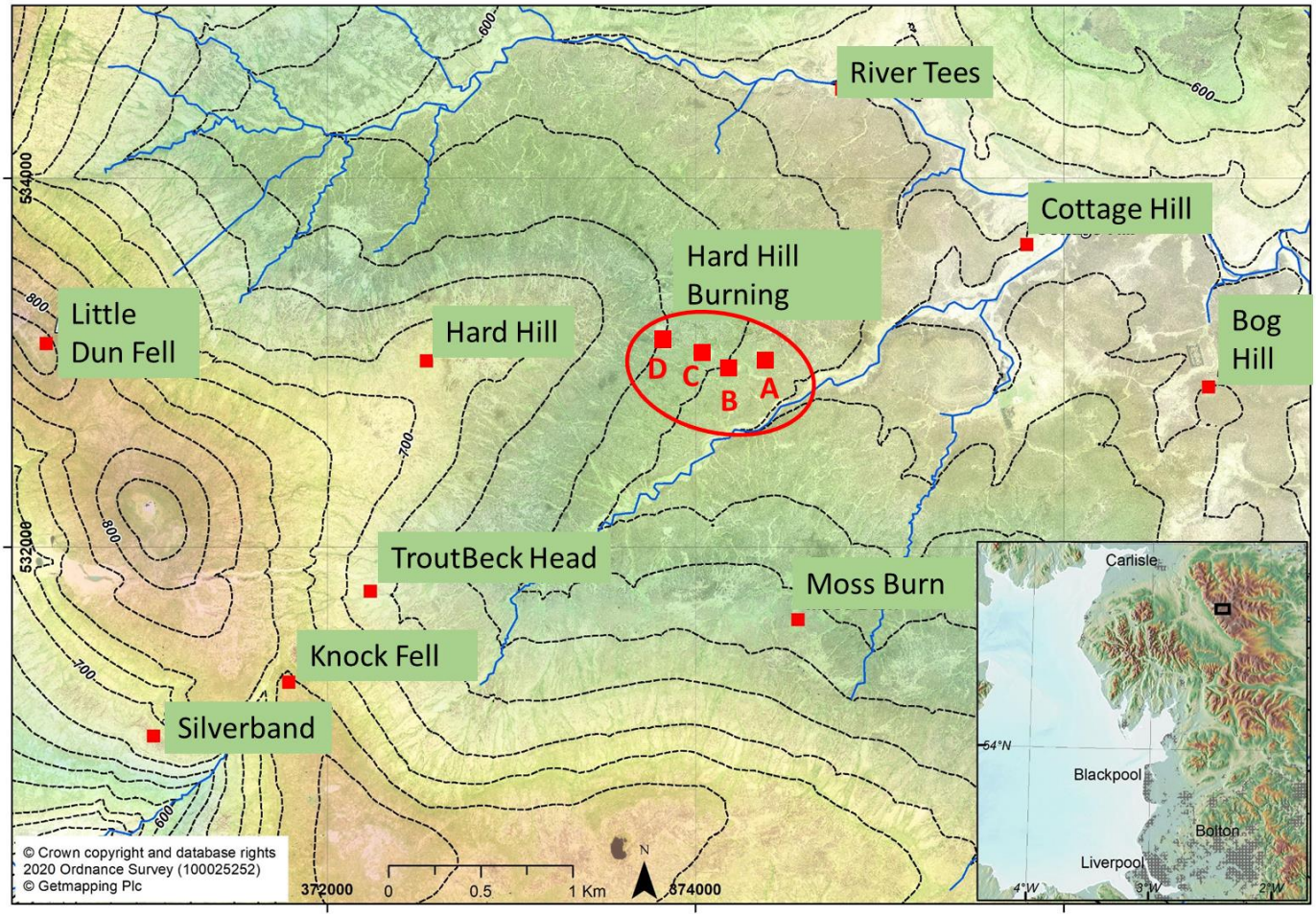


Fig. S1. General location of Moor House NNR (inset) and the geographical locations of all vegetation monitoring experiments.

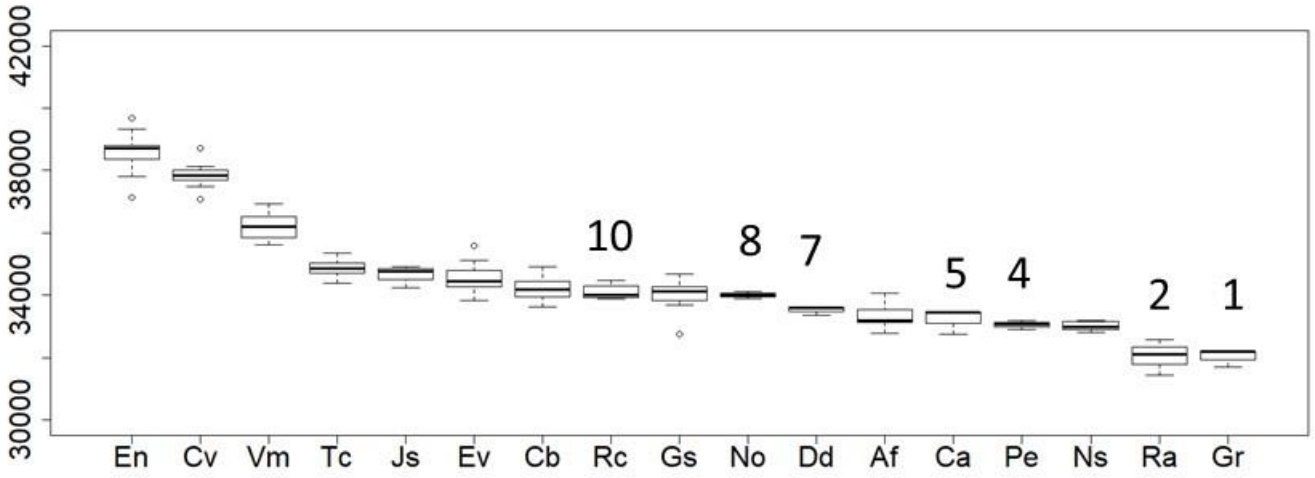
Fig. S2. Boxplots illustrating the relationships detected in a study of the relative differences in leaf properties of range of species in the Moor House grazing experiments. Species are ranked via effect size relative to the intercept species (species at the left hand end of axis 1, see Tables S4-S6). The rank of the seven focal species (Table 1) are also illustrated.

Species codes: Af = *Avellana flexuosa*, Cv = *Calluna vulgaris*, Cb = *Carex bigelowii*, Ca = *Chamaenerion angustifolium*, Dd = *Dryopteris dilatata*, En = *Empetrum nigrum*, Ev = *Eriophorum vaginatum*, Gs = *Galium saxatile*, Gr = *Geum rivale*, Js = *Juncus squarrosus*, Ns = *Nardus stricta*, No = *Narthecium ossifragum*, Pe = *Potentilla erecta*, Rc = *Rubus chamaemorus*, Ra = *Rumex acetosa*, Tc = *Trichophorum cespitosum*, Vm = *Vaccinium myrtillus*.

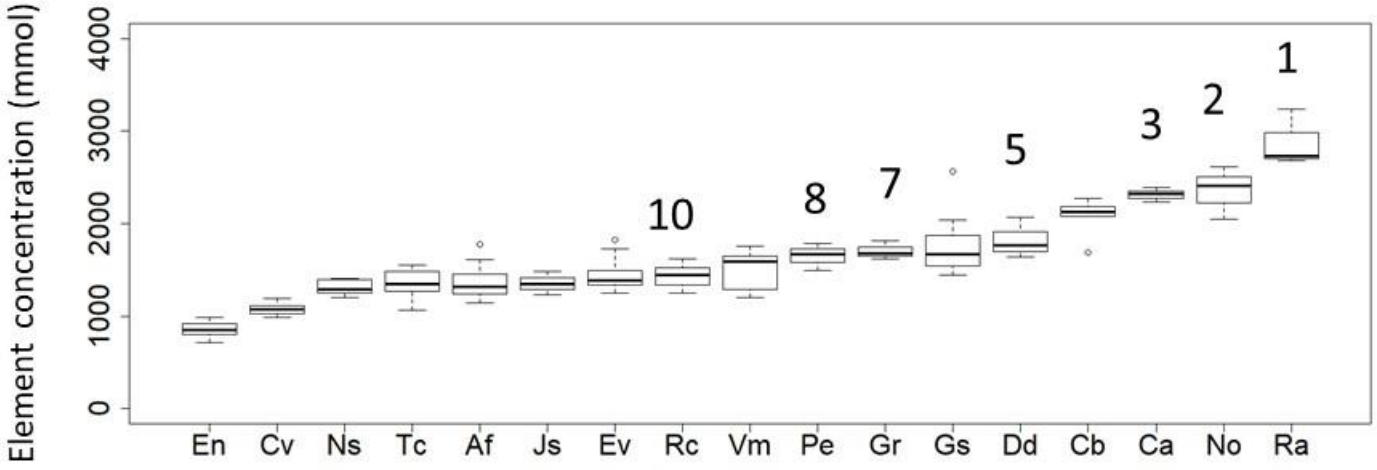
Panel 1: Macro-nutrient concentrations, (a) Carbon, (b) Nitrogen and (c) Phosphorus;
Panel 2: Major cation concentrations, (a) Potassium, (b) Sodium and (c) Calcium;
Panel 3: Digestibility variables, (a) Neutral Digestible Fibre (NDF), (b) DOMD (energy) and (c) Protein;
Panel 4: Micro-nutrient concentrations, (a) Sulphur, (b) Iron, (c) Chlorine and (d) Zinc;
Panel 5: Micro-nutrient concentrations (continued), (a) Manganese, (b) Nickel, (c) Copper and (d) Molybdenum;
Panel 6: (a) C: ratio (decomposability), and (b) Silicon (palatability).

Panel 1: Macro-nutrient concentrations

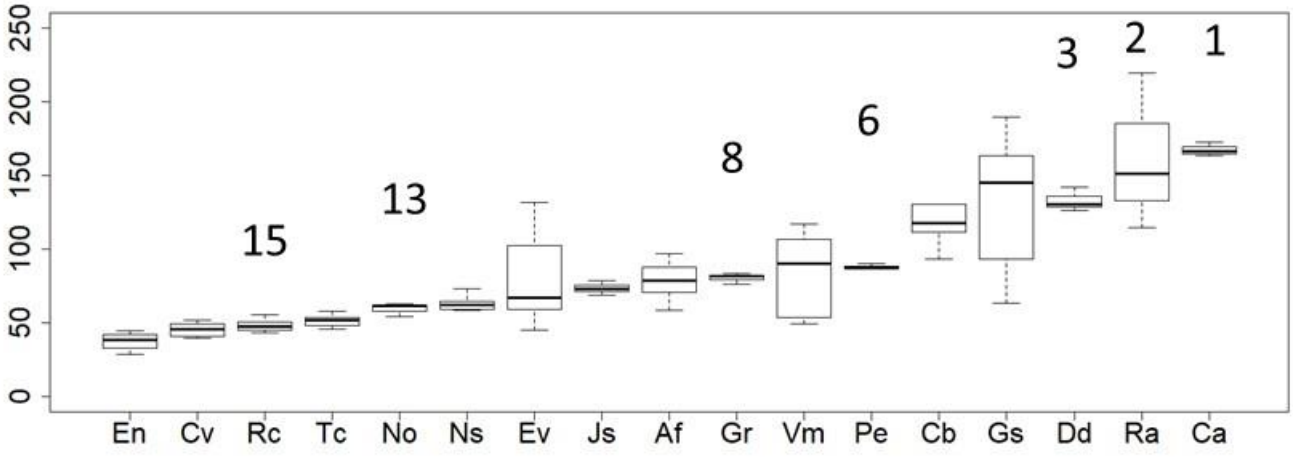
(a) Carbon - C



(b) Nitrogen - N



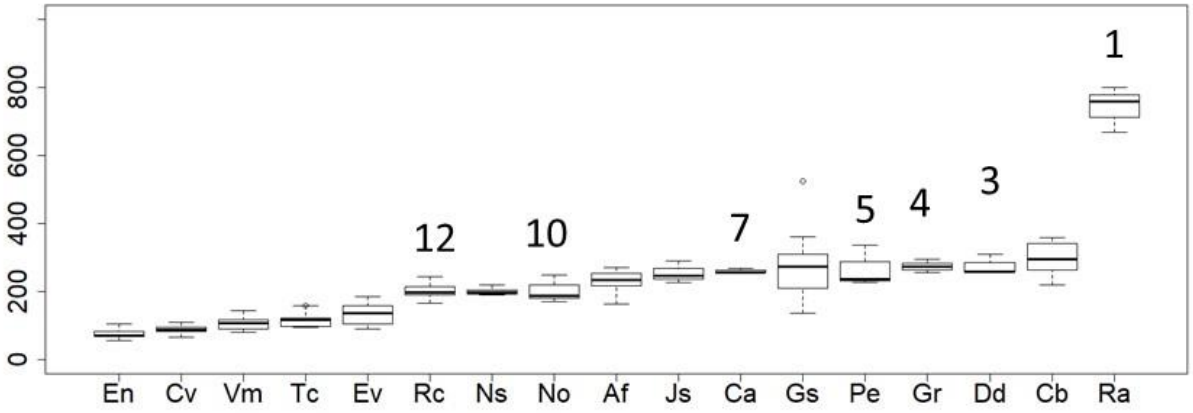
(c) Phosphorus - P



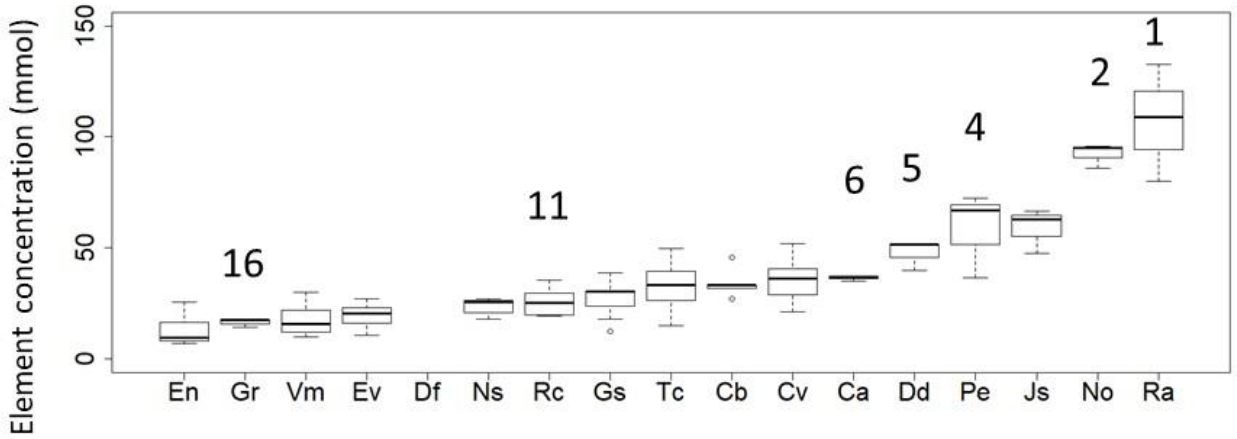
Species

Panel 2: Major cation concentrations, (a) Potassium, (b) Sodium and (c) Calcium

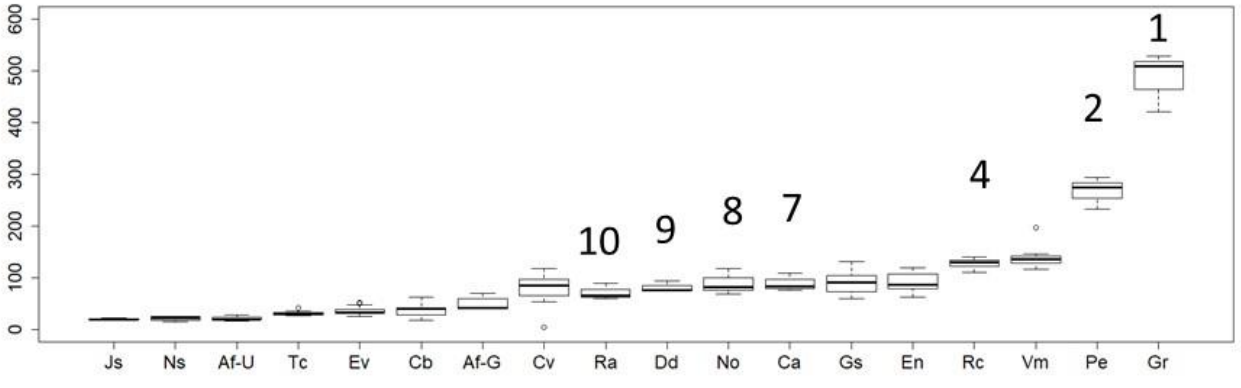
(a) Potassium - K



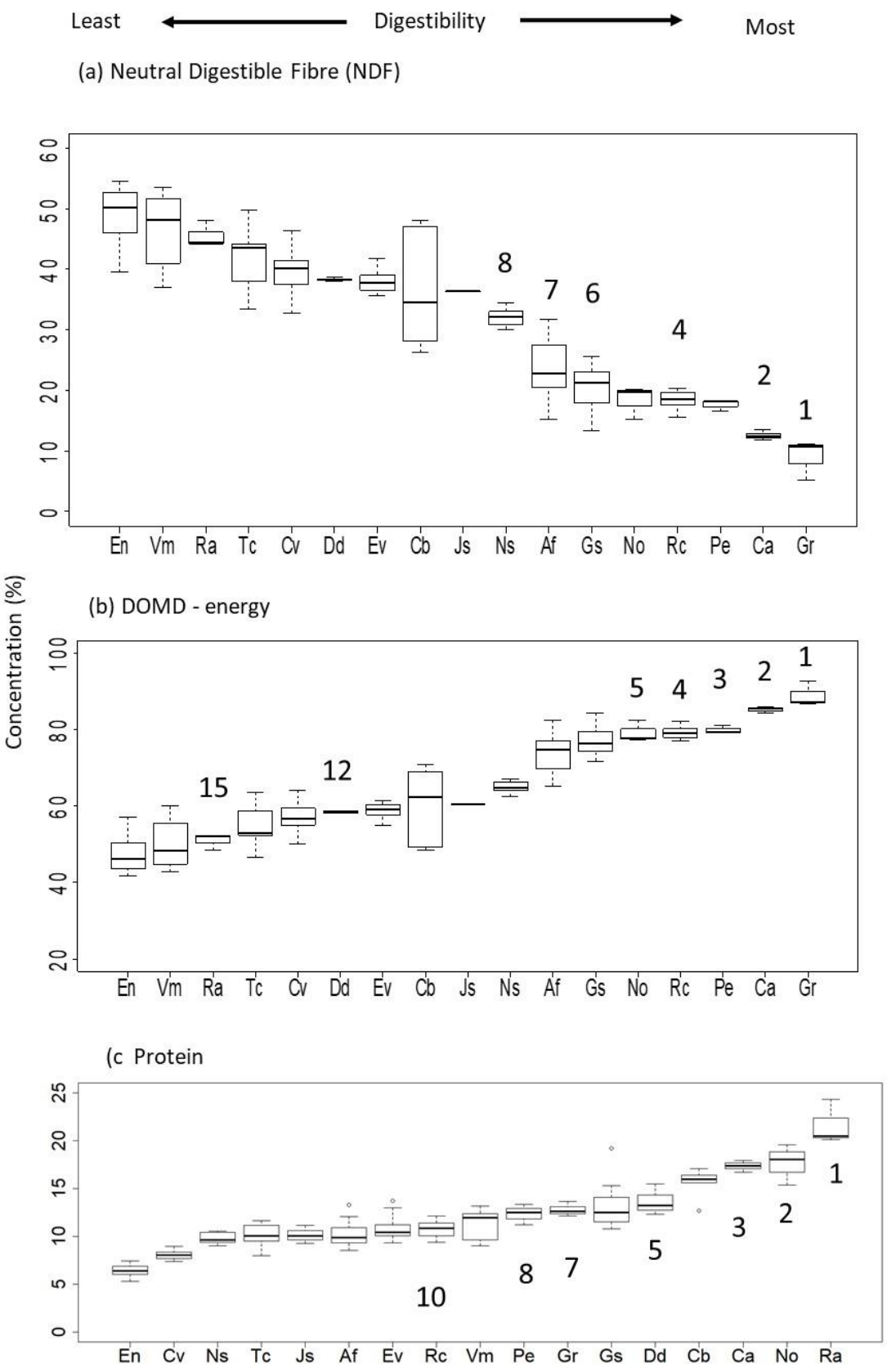
(b) Sodium -Na



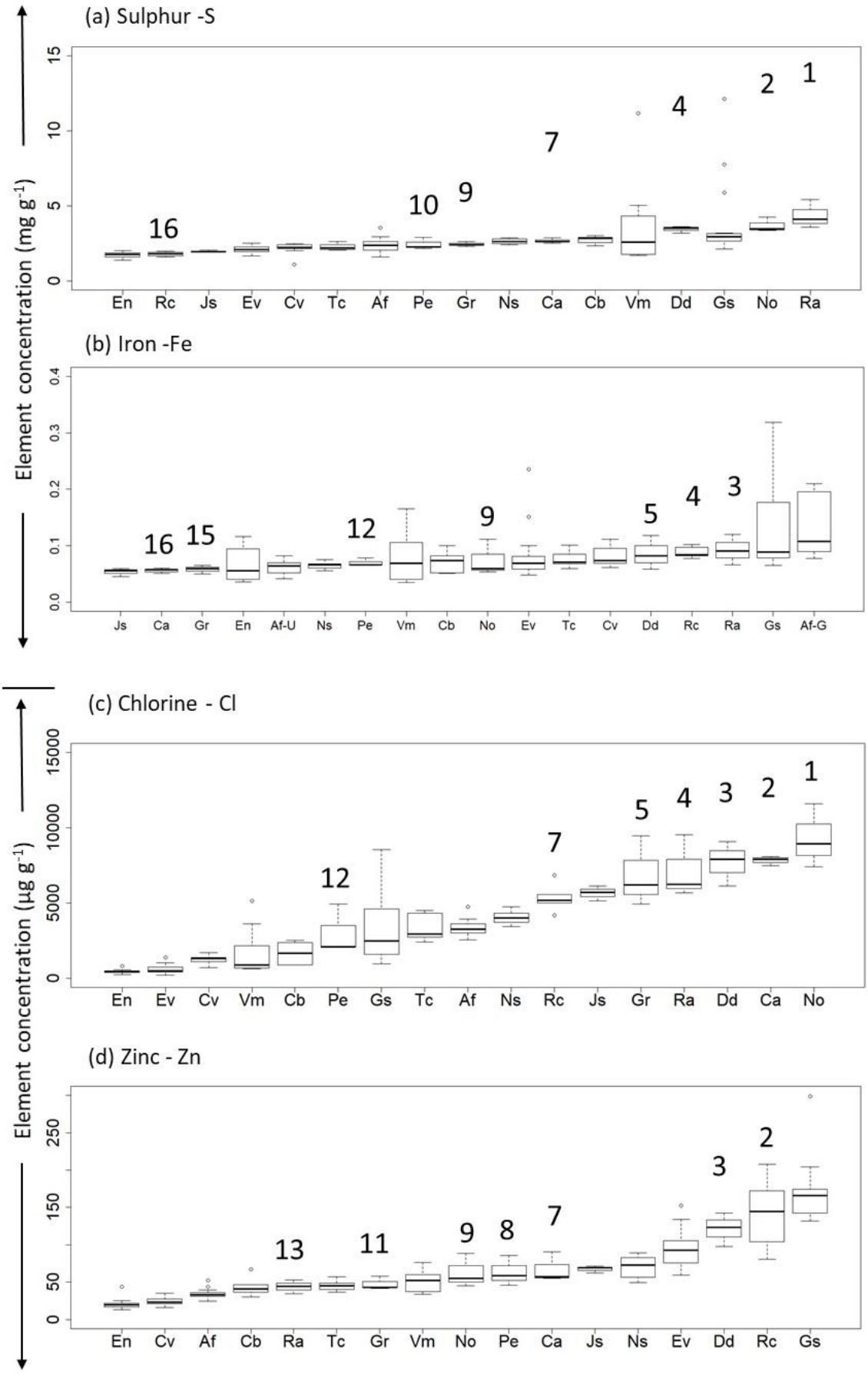
(c) Calcium - Ca



Panel 3: Digestibility variables, (a) Neutral Digestible Fibre (NDF), (b) DOMD (energy) and (c) Protein

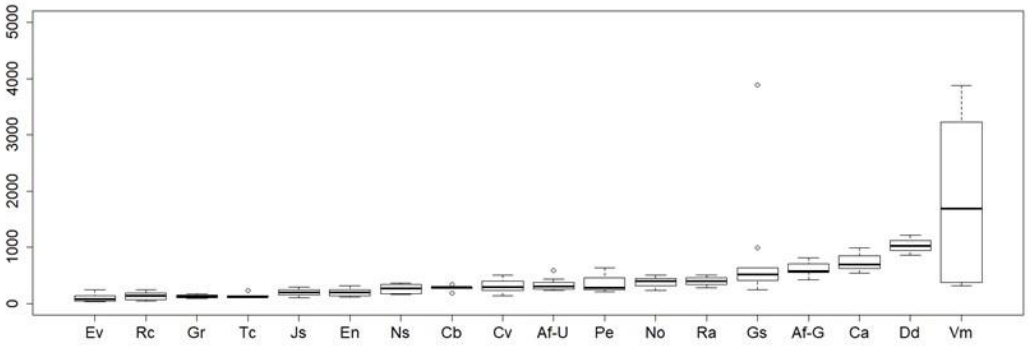


Panel 4: Micro-nutrient concentrations, (a) Sulphur, (b) Iron, (c) Chlorine and (d) Zinc

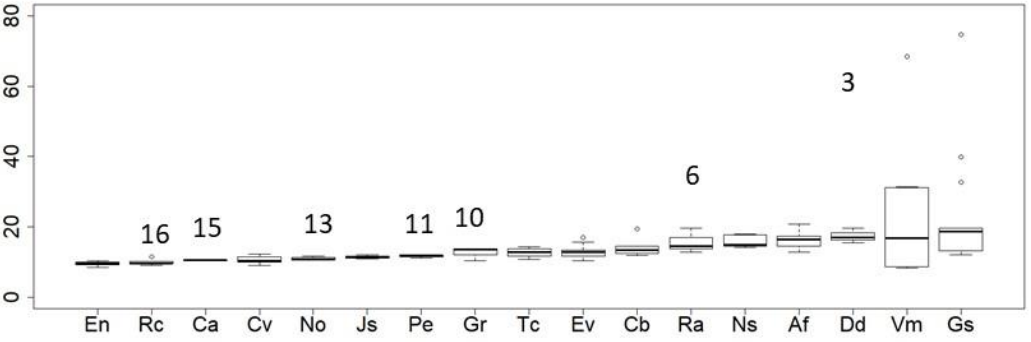


Panel 5: Micro-nutrient concentrations (continued), (a) Manganese, (b) Nickel, (c) Copper and (d) Molybdenum

(a) Manganese - Mn

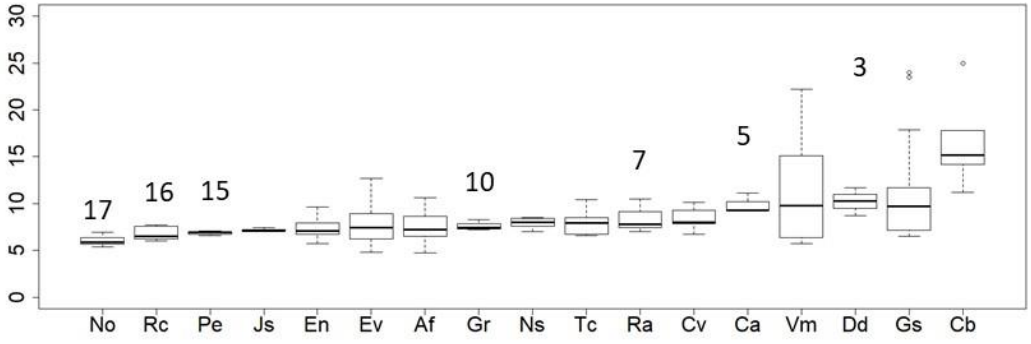


(b) Nickel - Ni

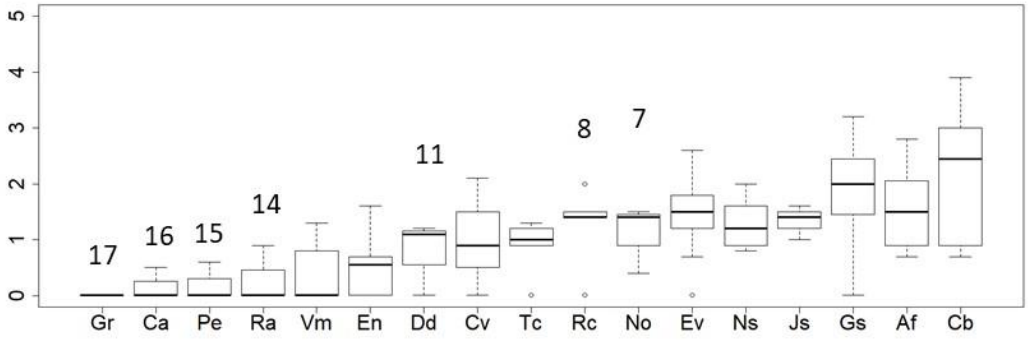


Element concentration (µg g^{-1})

(c) Copper - Cu



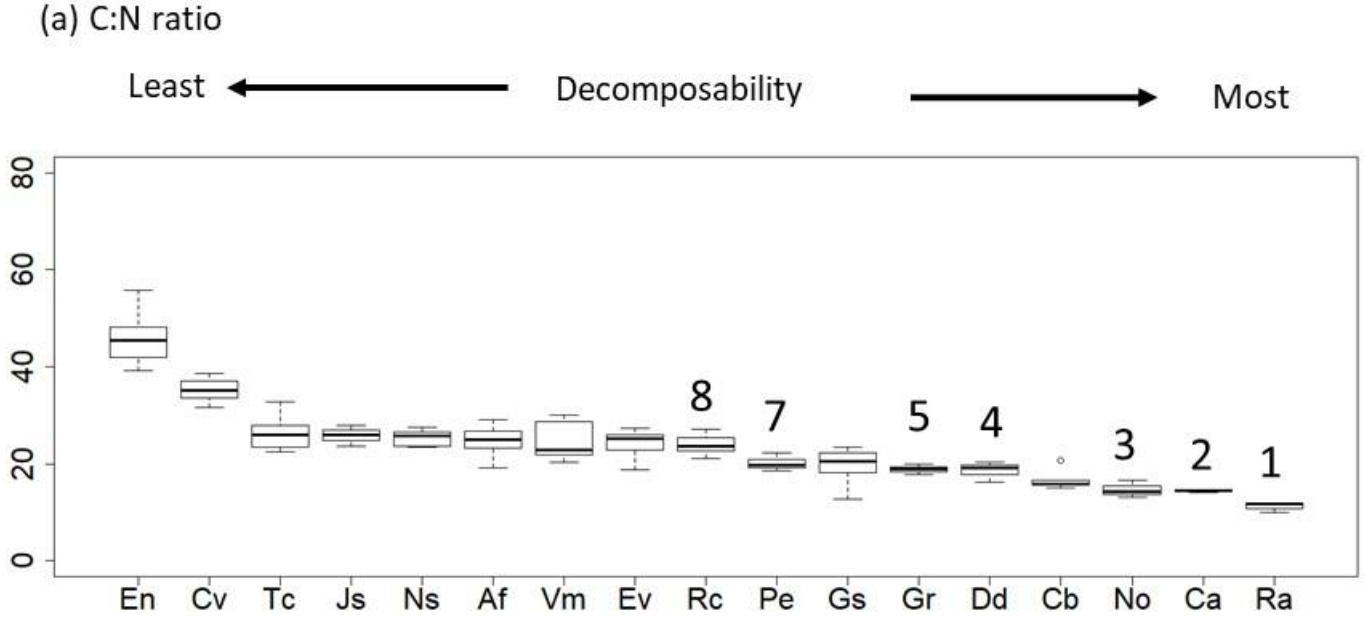
(d) Molybdenum - Mb

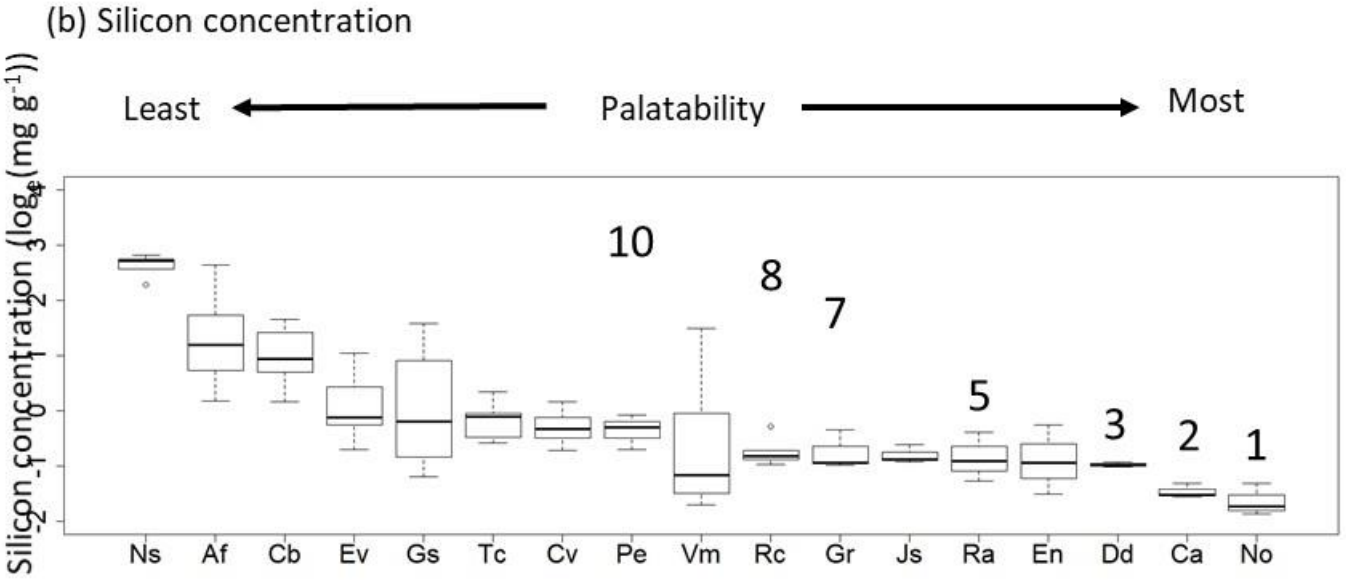


Species

1

Panel 6: (a) C: ratio (decomposability), and (b) Silicon (palatability)





Species

2

1

2

3

4

5

1

1